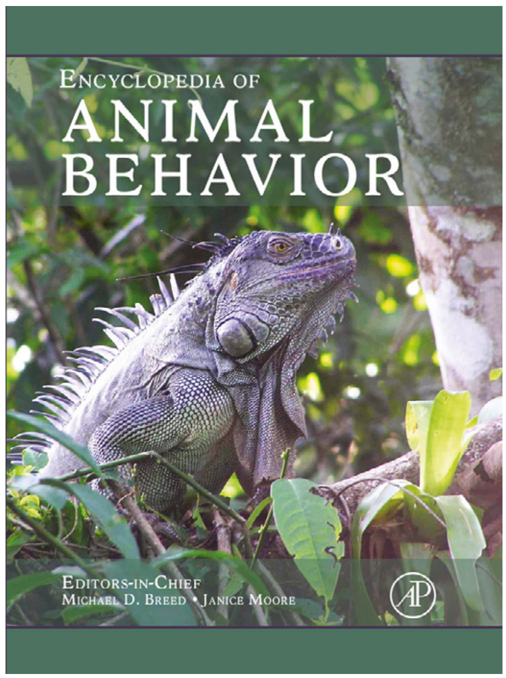

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Reproductive Skew, Cooperative Breeding, and Eusociality in Vertebrates: Hormones

W. Saltzman, University of California, Riverside, CA, USA

Introduction

Reproductive skew refers to the degree of asymmetry in the distribution of direct reproductive success among individuals within a social group. In high-skew societies, direct reproduction is monopolized within one or both sexes by one or a small subset of behaviorally dominant individual(s), whereas low-skew societies are characterized by a more equitable distribution of reproduction among all adult group members. Numerous theoretical models have been developed to explain the evolution and maintenance of reproductive skew. Simultaneously, considerable work has been devoted to determine the behavioral and hormonal mechanisms generating asymmetric reproductive success in high-skew societies.

High-skew societies are exemplified by cooperative breeding systems, including their most extreme manifestation, eusociality. Strictly speaking, cooperative breeding refers to any breeding system in which some individuals provide alloparental care for the offspring of other animals. These so-called helpers or alloparents may be male or female, related or unrelated to the breeding pair, and adult or immature. Among singular cooperative breeders – that is, species in which reproduction is limited to one female within each social group – helpers are often reproductively inactive, adult or subadult offspring of the breeding pair. Thus, additional common characteristics of singular cooperative breeding systems are delayed dispersal from the natal group and delayed or suppressed reproduction in helpers. Eusociality is a form of cooperative breeding characterized by extremely high reproductive skew and, according to some definitions, occurrence of irreversibly distinct behavioral castes. Cooperative breeding has been identified in a broad diversity of taxa, including insects, arachnids, crustaceans, fish, birds, and mammals, whereas eusociality has traditionally been considered to occur only among insects, especially some species of hympenoptera, isoptera, hemiptera, and thysanoptera. More recently, however, several species of sponge-dwelling shrimps (*Synalpheus*) and two mammalian species, the naked mole-rat (*Heterocephalus glaber*) and the Damaraland mole-rat (*Cryptomys damarensis*), have also been characterized as eusocial.

The mechanisms underlying both the suppression of reproduction and the performance of parental-like behavior by nonbreeding alloparents have generated considerable interest among behavioral endocrinologists and behavioral ecologists. Here, I focus on the hormonal aspects of these two hallmarks of high-skew vertebrate societies.

Hormonal Mechanisms of Reproductive Inhibition in Eusocial/Cooperative Breeding Systems

Failure of adult individuals to breed can be mediated by inhibition of reproductive behavior, suppression of reproductive physiology, or a combination of the two. Behavioral mechanisms may involve inbreeding avoidance in animals living with their natal families or interference in mating behavior. Physiological suppression typically involves dysfunction of the hypothalamic–pituitary–gonadal endocrine axis and may be manifest in impairments in gonadal endocrine function, gametogenesis, and pregnancy maintenance. Both behavioral and physiological mechanisms of reproductive failure can be conceptualized as being either imposed on subordinate individuals (i.e., helpers) by dominants, to the benefit of the dominant but at a cost to the subordinate, or self-imposed by subordinates as an adaptive response to specific organismal, social, or environmental cues.

The proximate mechanisms underlying reproductive inhibition have been investigated in numerous cooperatively breeding birds and mammals, and at least one cooperatively breeding fish. Most of these studies have compared activity of the hypothalamic–pituitary–gonadal axis between breeders and nonbreeders to discern whether or not nonbreeders are physiologically capable of reproducing. Briefly, in breeding adults, the hypothalamus secretes gonadotropin-releasing hormone (GnRH), which stimulates the anterior pituitary to secrete luteinizing hormone (LH) and follicle-stimulating hormone (FSH). These two gonadotropins, in turn, exert stimulatory effects on the gonads, promoting both gametogenesis and production of gonadal steroids (primarily testosterone in males, estradiol and progesterone in females) and peptide hormones (e.g., inhibin). Gonadal hormones feed back to the brain and pituitary to regulate secretion of GnRH, LH, and FSH. Reproductive impairments in subordinates can be caused, potentially, by dysfunction at the level of the gonads, pituitary, hypothalamus, or higher brain structures.

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Reproductive Suppression in Male Cooperative Breeders

Studies of cooperatively breeding birds provide mixed evidence for suppression of the hypothalamic–pituitary–testicular axis. In some species (e.g., red-cockaded woodpecker, *Picoides borealis*; Harris's hawk, *Parabuteo unicinctus*), circulating concentrations of testosterone or total androgens do not differ between male breeders and adult male helpers. In others (e.g., bell miner, *Manorina melanophrys*; superb fairy-wren, *Malurus cyaneus*), helpers have consistently lower levels of testosterone than breeders, and in still others (e.g., pied kingfisher, *Ceryle rudis*), testosterone levels are low in male helpers that are sons of one or both breeders (i.e., primary helpers), but not in male helpers that are unrelated to the breeding pair (i.e., secondary helpers). Even in species in which male helpers have low testosterone levels compared to breeders, testosterone levels may undergo seasonal changes comparable to those in breeding males, and LH concentrations in helpers may not be reduced, suggesting that the hypothalamic and pituitary components of the gonadal axis are not impaired. Moreover, low testosterone levels in these helpers are not necessarily associated with impaired sperm production or infertility.

Cooperatively breeding male mammals show little evidence of suppressed reproductive physiology. Circulating or excreted testosterone concentrations do not differ reliably between breeders and nonbreeders in a number of cooperative rodents (e.g., Damaraland mole-rat; Mongolian gerbil, *Meriones unguiculatus*), carnivores (e.g., dwarf mongoose, *Helogale parvula*; gray wolf, *Canis lupus*), and primates (e.g., common marmoset, *Callithrix jacchus*; cotton-top tamarin, *Saguinus oedipus*). Thus, reproductive inhibition in most cooperatively breeding male mammals appears to be mediated exclusively by behavioral inhibition. One noteworthy exception is the eusocial naked mole-rat, in which nonbreeding males show significant reductions in plasma LH levels, urinary testosterone levels, sperm counts, and sperm motility as compared to breeders.

Reproductive Suppression in Female Cooperative Breeders

Relatively little is known about the mechanisms of female reproductive inhibition in avian cooperative breeders, perhaps because many cooperatively breeding birds have only male helpers. In the few studies that have been performed on avian female helpers, no clear pattern has emerged. Female helpers have been found to have low circulating LH and estradiol concentrations as compared to breeding females (Harris's hawk); smaller ovarian follicles and, in helpers unrelated to the breeding pair but not in related helpers, lower LH levels than breeders (white-browed sparrow-weaver, *Plocepasser mahali*); or smaller follicles and, in some years, lower estradiol levels than breeders, but no differences in baseline or GnRH-stimulated LH levels (Florida scrub jay, *Aphelocoma coerulescens*).

Female mammals have much higher costs of reproduction than males, mainly as a result of lactation, and are much less able to breed surreptitiously. Consequently, it might be predicted that subordinate females in cooperative mammalian societies would be under stricter physiological suppression of reproduction than subordinate males. Data from numerous species support this prediction. In many species (e.g., common marmoset, cotton-top tamarin, naked mole-rat, Damaraland mole-rat), many, if not all, female helpers fail to ovulate and have impaired ovarian steroidogenesis, as a consequence of diminished gonadotropic stimulation of the ovaries. In others (e.g., African wild dog, *Lycaon pictus*; meerkat, *Suricata suricatta*; dwarf mongoose), helpers might undergo ovulatory cycles, but have lower circulating or excreted estrogen levels than breeders.

Social Determinants of Reproductive Suppression in Cooperative Breeders

Unlike the eusocial insects, cooperatively breeding vertebrates do not undergo irreversible differentiation into permanent reproductive morphs. Instead, reproductive inactivity in helpers, whether behaviorally or physiologically mediated, is typically dependent on age and social context. The specific social determinants of reproductive failure in nonbreeding helpers are generally not known. In offspring of the breeding pair, lack of sexual stimulation from an unrelated, opposite-sex adult can potentially delay reproductive maturation in young animals or diminish hypothalamic–pituitary–gonadal function in mature adults, as well as inhibiting sexual behavior. Alternatively or additionally, reproductive physiology may be suppressed in response to agonistic interactions with dominant individuals, most likely the same-sex breeder, or in response to specific sensory cues, such as chemical signals from a dominant animal. Studies designed to tease apart the relative roles of inbreeding avoidance and rank-related reproductive suppression indicate that the relative importance of these two factors may vary among species and perhaps between the sexes within species.

Reproductive Suppression and Stress in Cooperative Breeders

Social subordination is often assumed to be inherently stressful, and stress-related physiological changes, such as increased secretion of the endogenous opioids (e.g., β-endorphin) from the pituitary, catecholamines (epinephrine

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and norepinephrine) from the sympatho-adrenomedullary system, and glucocorticoids (cortisol and corticosterone) from the adrenal cortex, can inhibit activity of the hypothalamic–pituitary–gonadal axis. Consequently, considerable interest has focused on the question of whether reproductive suppression in subordinate cooperative breeders is stress-induced. Many studies have examined potential differences in activity of the hypothalamic–pituitary–adrenal (HPA) endocrine axis – especially circulating or excreted glucocorticoid concentrations – between breeders and nonbreeders. Activation of the HPA axis involves secretion of the neuropeptide corticotropin-releasing hormone (CRH, also referred to as corticotropin-releasing factor, CRF) from the paraventricular nucleus of the hypothalamus into the hypothalamo-hypophyseal portal vasculature. At the anterior pituitary, CRH stimulates the secretion of adrenocorticotropic hormone (ACTH) from corticotrope cells. ACTH in turn stimulates the zona fasciculata of the adrenal cortex to secrete glucocorticoid hormones, which elicit a broad range of effects in the brain and body.

Most studies of cooperatively breeding and eusocial vertebrates have found either no differences in circulating or excreted glucocorticoid levels in association with breeding status (e.g., male and female white-browed sparrow-weaver; male and female gray wolf), or elevated levels in breeders as compared to nonbreeders (e.g., female common marmoset; male and female African wild dog; male daffodil cichlid, *Neolamprologus pulcher*). Thus, reproductive inhibition in these subordinates is not thought to result from generalized stress and may instead be mediated by more specialized neuroendocrine mechanisms. The final common pathway for many of these mechanisms may be alterations in hypothalamic secretion of GnRH, leading to suppressed release of gonadotropins from the pituitary and, consequently, to impaired gametogenic, endocrine, and/or ovulatory function in the gonads. Several exceptions to this pattern have been reported, however, including male and female naked mole-rats and female meerkats, in which reproductive inhibition in helpers is associated with elevated glucocorticoid levels. Even in these species, though, stress and glucocorticoids have not been shown experimentally to play a causal role in reproductive inhibition.

Hormonal Mechanisms of Reproductive Skew in Noncooperative Breeding Systems

Although reproductive skew is most pronounced in cooperatively breeding and eusocial species, moderate asymmetries in the distribution of direct reproduction within social groups may occur in other types of vertebrate breeding systems. Are the mechanisms that bias reproductive outcomes in these lower-skew societies quantitatively or qualitatively different from those that more strictly limit reproductive success to a small number of individuals in high-skew societies?

Reproductive Suppression in Male Noncooperative Breeders

Both reproductive success and circulating testosterone concentrations may differ markedly among males in noncooperative societies, such as multimale groups or lek-polygyny mating systems. Nonetheless, studies examining the relationship between reproductive success and testosterone levels have not yielded a consistent pattern. Several explanations have been proposed. First, circulating testosterone levels within the normal range do not necessarily show a linear relationship with measures of spermatogenesis or sexual behavior, and virtually all adult (and subadult) males in these species are likely to have breeding-season testosterone levels high enough to support both physiological and behavioral components of reproduction. On the other hand, testosterone levels may correlate with, and may be strongly influenced by, success in intermale agonistic encounters, such as dominance-related and territorial interactions (i.e., the Challenge Hypothesis), which may or may not correlate with reproductive success. Furthermore, experimental studies have shown that while elevated testosterone levels may enhance some aspects of reproductive behavior, such as courtship and territorial defense, they may inhibit others, such as feeding of nestlings by avian fathers.

The lack of correspondence between testosterone levels and reproductive success suggests that in many species, male reproductive skew is mediated primarily or entirely by behavioral, rather than physiological means. Some exceptions exist, however, in which low-ranking males exhibit such physiological impairments – likely mediated by the hypothalamic–pituitary–testicular axis – as reduced sperm number, sperm motility, or semen volume (e.g., sheep, *Ovis aries*; house mouse, *Mus musculus*), delayed puberty (e.g., savannah baboon, *Papio cynocephalus*; sheep), or inhibited development of secondary sexual characteristics (e.g., orangutan, *Pongo pygmaeus*; European minnow, *Phoxinus phoxinus*) can presumably reduce lifetime reproductive success.

Reproductive Suppression in Female Noncooperative Breeders

Noncooperative female vertebrates rarely exhibit the complete, socially-induced suppression of ovulatory activity found in some cooperative/eusocial species. Instead, reproductive skew among females in these societies may be mediated by mechanisms, often stress-induced, that delay puberty (e.g., house mouse), inhibit sexual behavior (e.g., rhesus macaque, *Macaca mulatta*), delay conception (e.g., savannah baboon), block implantation (e.g., white-footed mouse, *Peromyscus leocopus*), induce spontaneous abortion or prenatal litter reduction (e.g., golden hamster, *Mesocricetus auratus*), or impair maternal care (e.g., ringtailed lemur, *Lemur catta*) in subordinate females. Such mechanisms can be activated by a variety of stressors such as agonistic interactions among females or reduced access to food or other resources.

Hormonal Mechanisms of Alloparental Care

A second aspect of cooperative breeding/eusociality of interest to behavioral endocrinologists, in addition to the mechanisms of reproductive curtailment in nonbreeding helpers, is the proximate control of alloparental behavior. Parental behavior in breeding individuals is activated by specific hormones (especially estrogen, progesterone, prolactin, and oxytocin) acting upon the brain while, in some cases, acting simultaneously upon peripheral structures (e.g., mammary glands, crop sac). In birds, the onset of parental behavior toward hatchlings is facilitated by the hormonal sequelae of incubation, whereas in mammals, the endocrine events stimulating the onset of maternal behavior are intimately linked to pregnancy, parturition, and lactation, processes that do not occur in nonbreeding helpers. Because cooperative breeding systems are characterized by nonbreeding individuals engaging in parental-like behavior, the question arises as to whether this alloparental behavior, like parental behavior, is activated by specific hormonal events. The identification of hormonal mechanisms regulating alloparenting, especially in birds, has also been considered crucial in determining whether alloparental behavior is evolutionarily distinct from parental behavior and results directly from natural selection, or whether it simply reflects a stereotyped response to cues from nestlings, which evolved in the context of parents provisioning their own offspring and which may not be dependent on hormonal priming. Thus, understanding the hormonal influences on alloparenting, if any, may elucidate both the proximate and ultimate causes of cooperative breeding.

Prolactin

Most studies of the endocrine correlates of alloparental behavior have focused on prolactin, a peptide released both within the brain and by the anterior pituitary into the general circulation. Prolactin has been demonstrated conclusively to play a key role in the onset of parental behavior in mammalian mothers and in avian mothers and fathers, and has been associated correlationally with paternal behavior in mammalian fathers in biparental species. Similarly, correlational evidence supports the hypothesis that prolactin promotes alloparental behavior in several cooperatively breeding birds and mammals: both inter- and intraspecific studies have found positive associations between alloparental behavior and prolactin concentrations in male and female helpers. In meerkats, for example, adult males have significantly higher circulating prolactin concentrations prior to a bout of 'babysitting' than prior to a bout of foraging, suggesting that prolactin might influence individual helpers' decisions to provide alloparental care. In Florida scrub jays and Harris's hawks, plasma prolactin levels in both breeders and nonbreeders rise during the incubation stage and correlate with individual differences in helping behavior. Prolactin secretion can be stimulated by incubation, however, or by contact with or exposure to nestlings/infants, and very few experimental studies have been conducted to determine whether prolactin plays a causal role in alloparenting. Thus, while prolactin remains the most obvious candidate for an 'alloparental hormone,' its role in the expression of alloparental care, if any, is not yet clear.

Testosterone

High circulating levels of testosterone have been shown to influence – usually, to inhibit – paternal behavior in a number of birds and mammals. Therefore, several studies of cooperative breeders have focused on testosterone in helpers as a possible determinant of alloparental care. No clear pattern has emerged in the relationship between individual alloparents' current testosterone levels and helping behavior. In male azure-winged magpies (*Cyanopica cyana*), endogenous circulating testosterone concentrations do not correlate with helping behavior, but treatment of male helpers with exogenous testosterone elevates their rates of feeding nestlings. In contrast, low endogenous testosterone levels in male Mongolian gerbils are associated with high alloparental responsiveness. More importantly, perhaps, exposure to androgens or other steroid hormones during the perinatal period is likely to permanently alter the propensity to provide alloparental care by exerting organizational effects on the central nervous system, especially in species that exhibit sex differences in alloparental behavior.

Pregnancy

In several cooperatively breeding mammals (e.g., common marmoset, meerkat, Mongolian gerbil), both dominant and subordinate females may commonly become infanticidal during pregnancy, presumably as a manifestation of female–female reproductive competition. The mechanisms underlying this pattern are not known but are likely to involve pregnancy-related hormonal changes.

Glucocorticoids

Few studies have addressed a possible relationship between glucocorticoid hormones and alloparental behavior. In meerkats, however, correlational evidence suggests that high glucocorticoid levels may increase pup-feeding rates by male helpers.

Future Directions

Clearly, much remains to be learned about the endocrinology of reproductive skew, cooperative breeding, and eusociality in vertebrates. While hormones undeniably play a role in limiting reproduction in at least some male and female cooperative breeders, the endocrine/neuroendocrine mechanisms underlying such effects, as well as the social or sensory cues activating these mechanisms, remain almost entirely unknown. Moreover, although rank-related differences in glucocorticoid concentrations have been reported in many cooperatively breeding vertebrates – often with dominant, breeding individuals exhibiting higher glucocorticoid levels than subordinate nonbreeders – nothing is known about the functional significance of these differences. Finally, our understanding of hormonal influences on alloparental care is rudimentary. Focused, experimental studies, ideally involving hormone manipulations, are needed to further elucidate the role of the endocrine system in determining reproductive and behavioral profiles of vertebrates living in high-skew societies.

See also: Caste Determination in Arthropods; Cooperation and Sociality; Fight or Flight Responses; Helpers and Reproductive Behavior in Birds and Mammals; Invertebrates: The Inside Story of Post-Insemination, Pre-Fertilization Reproductive Interactions; Mammalian Female Sexual Behavior and Hormones; Pair-Bonding, Mating Systems and Hormones; Parental Behavior and Hormones in Mammals; Parental Behavior and Hormones in Non-Mammalian Vertebrates; Reproductive Skew; Sexual Behavior and Hormones in Male Mammals.

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