



Physiological mechanisms mediating patterns of reproductive suppression and alloparental care in cooperatively breeding carnivores



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ABSTRACT

Although cooperation represents a long-standing evolutionary puzzle, field studies on social carnivores have contributed greatly to our understanding of the selective forces favoring cooperative breeding. Despite these insights, our grasp of the proximate mechanisms facilitating cooperation in carnivores remains surprisingly limited. Here we provide an overview of our current knowledge of the endocrine mechanisms mediating cooperative breeding in terrestrial species belonging to the mammalian order Carnivora. We focus primarily on aspects of reproductive suppression and alloparental care. We find few studies on the topic, with some of the best studies focusing on the behavioral endocrinology of cooperative breeding in canids (dogs) and herpestids (mongooses). Overall, these studies suggest that breeding females typically have higher circulating levels of estrogen, luteinizing hormone, progesterone, and prolactin than do non-breeding adult females. We also find that among males, testosterone levels are often elevated in breeders compared to non-breeding adult males. The effect of glucocorticoids on reproductive suppression in carnivores appears to be sex-specific: breeding males typically have higher glucocorticoid levels than their non-breeding subordinates, but there is no clear pattern for breeding females. Finally, elevated levels of prolactin and oxytocin are consistently associated with alloparental care in cooperatively breeding carnivores, whereas testosterone and glucocorticoids are often lower in individuals who participate in alloparenting. Taken together, our synthesis elucidates striking gaps in our knowledge of carnivore physiology, especially the endocrine mechanisms promoting alloparental care, and we identify important areas for future research.

1. Introduction

The vast majority of species (~85–90%) belonging to the mammalian order Carnivora (here referred to as “carnivores”) are solitary such that conspecifics interact only to mate or raise young [1,2]. Here we focus on “social carnivores,” those terrestrial members of the order Carnivora whose individuals interact frequently with one another, forming social groups called societies [3]. Specifically, these species regularly cooperate with group-mates to hunt large game, defend resources, guard against predators, attack others, and/or rear young [4,5]. Researchers have long recognized the social carnivores as an important taxonomic group for understanding the evolutionary origins and maintenance of cooperation [6–9].

Cooperatively breeding members of the social carnivores are particularly fascinating because their social systems are characterized by alloparental care and often by some degree of reproductive suppression. Alloparental care, defined as any investment in the evolutionary fitness

of non-descendent offspring (e.g., born to others), includes all behaviors in which individuals guard, groom, carry, play with, feed, or nurse the offspring of others [10]. In contrast, reproductive suppression in cooperative breeders occurs when individuals beyond the age of sexual maturity fail to raise young of their own, regardless of the mechanism involved [11]. The extent of cooperative care of young varies widely among carnivore species, ranging from joint territorial defense to the nursing and provisioning of unrelated offspring [12]. The degree of care often varies with the extent of reproductive suppression within social groups [13]. Social carnivores that engage in some form of cooperative breeding include species belonging to the canid (dog), felid (cat), herpestid (mongoose), hyaenid (hyena), mustelid (weasel), and procyonid (coati) families [14,15].

Carnivores are typically categorized as communal breeders, facultative cooperative breeders, or obligate cooperative breeders based on the degree to which non-parents assist in the cooperative care of offspring born to others, regardless of how breeding is shared within the

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group [12,16]. Among communal breeders, such as African lions (*Panthera leo*), spotted hyenas (*Crocuta crocuta*), and banded mongooses (*Mungos mungo*), most females breed during each reproductive cycle and participate in some alloparental care, although temporarily non-breeding females and males may also contribute to the care of young born to the group [17]. In facultative cooperative breeders, such as black-backed jackals (*Canis mesomelas*) and Arctic foxes (*Vulpes lagopus*), both parents and non-breeding helpers alike care for the young, but the number of helpers is small, and parents may successfully raise their young with no helper assistance [4]. Obligate cooperative breeders, such as African wild dogs (*Lycaon pictus*) and meerkats (*Suricata suricatta*), require assistance from non-breeding helpers to successfully raise offspring; in these groups, non-breeding helpers often provide the majority of care to the young, and their number typically exceeds the number of breeders within these groups [15].

The benefits of cooperative breeding for offspring survival and fitness are widely established among many taxa, including various social carnivore species [18–22]. In contrast to our broad understanding of the evolutionary function of cooperative breeding [23], our knowledge of the physiological mechanisms mediating reproductive suppression and alloparental care in mammals remains surprisingly limited [24]. Social carnivores offer a rare opportunity to study the physiological mechanisms of cooperative breeding within a comparative framework. Carnivores face a unique set of ecological pressures, such as extreme fluctuations in prey availability and high protein diets, which may have led to the evolution of different physiological trade-offs than those experienced by cooperative breeders in other mammalian taxa [25]. Our goal here is therefore to provide an updated synthesis of the hormonal aspects of cooperative breeding, namely reproductive suppression and alloparental care, in social mammals within the order Carnivora. We aim to identify key gaps in our knowledge about the physiological basis for cooperation in social carnivores in an effort to propel this area of research forward within a comparative context.

2. Reproductive suppression

Sexually mature adults of either sex may fail to breed when reproductive behavior is inhibited, reproductive physiology is suppressed, or both occur. Behavioral inhibition includes avoidance of inbreeding in animals living in natal groups [26,27], direct interference in mating attempts [28,29], infanticide [30,31], or the inability to find a suitable mate [27,32]. Physiological suppression usually involves dysfunction of the hypothalamic-pituitary-gonadal (HPG) axis, leading to degradation in gonadal endocrine function, gametogenesis, and maintenance of pregnancy [33].

Most mammalian studies of the physiological mechanisms mediating reproductive inhibition have examined HPG axis activity to determine whether non-breeders are physiologically capable of reproducing. In breeders, gonadotropin-releasing hormone (GnRH) is released from neurosecretory cells in the hypothalamus, causing the pituitary to secrete luteinizing hormone (LH) and follicle-stimulating hormone (FSH). In turn, LH and FSH stimulate the gonads to facilitate gametogenesis and the production of gonadal steroids such as testosterone in males and estrogen and progesterone in females. These gonadal hormones then feed back to the brain and pituitary, which further regulate secretion of GnRH, LH, and FSH [34]. Dysfunction at any point in this loop can potentially impair reproduction, creating a non-breeding adult [33].

Failure to breed in mammals may thus arise from many physiological causes. In males, for example, inadequate levels of GnRH, FSH, or LH may prevent spermatogenesis or lead to insufficient testosterone, which could reduce mating behavior [35]. In females, the suppression of reproductive function may occur if inadequate estrogen buildup in the female fails to signal receptivity to males, if the absence of a peak in GnRH or LH levels produces unsuccessful ovulation, or if insufficient levels of progesterone fail to establish or maintain pregnancy [11].

Non-reproductive females may also display pseudopregnancy, an ovulatory but non-pregnant state that includes elevated progesterone levels and physical changes such as an extended abdomen and lactation [36,37].

2.1. Stress-induced reproductive suppression

In addition to those actions regulated by gonadal steroids, stress hormones (glucocorticoids, GCs) may be involved in regulating reproductive suppression and alloparental care in mammals. GCs, which are released from the adrenal cortex, can suppress HPG axis activity through inhibition of GnRH, and thus LH and FSH, in both males and females [34]. Pioneering studies showed that losing fights triggers a significant increase in circulating levels of GCs in captive rodents [38,39]. These studies generated the ‘stress of subordination’ hypothesis, which posits that social stressors act to physiologically suppress subordinate reproduction in cooperative breeders [40,41]. However, while data from some free-living species support this hypothesis (e.g., olive baboons, *Papio anubis* [42]), a review by Creel [40] reported that for five of the six studied species of free-living mammalian cooperative breeders, dominants had higher GCs than subordinates. These data initiated the ‘stress of dominance’ hypothesis, which suggests that dominant individuals endure the highest degree of social stressors, likely because aggression is stressful to both the perpetrator and the recipient [43]. In the wild, dominant animals of many species engage in higher rates of aggressive behavior than subordinate group members, as dominants must participate in aggressive behavior to maintain their status while subordinates can potentially evade aggression via avoidance of dominants [40]. These studies have clarified that dominance hierarchies, social stability, and other features that differentiate wild groups from captive ones likely influence this endocrine relationship [44].

More recent work has suggested that the processes used to acquire and maintain social dominance, not the dominant or subordinate status itself, may determine the physiological mediation of reproductive suppression [43]. For example, although subordinates may have lower overall GC levels than dominants, their GC levels may spike at much higher concentrations than dominants while they are contesting status, and it is these higher GC concentrations which may suppress reproduction in subordinates [45]. Clearly, further research will be required to fully elucidate the role of GCs in reproductive suppression in cooperatively breeding mammals, and studies of social carnivores may aid in these efforts.

3. Alloparental care

The physiological mechanisms providing the proximate control of alloparenting present a second avenue for understanding mammalian cooperative breeding behavior. In breeding females, specific hormones such as estrogen, progesterone, prolactin, and oxytocin act upon the brain and peripheral structures (i.e. mammary glands) to promote maternal care [46,47]. These endocrine stimuli are closely linked to pregnancy, parturition, and lactation [34]. However, these processes do not occur in the non-breeding helpers engaging in maternal-like behavior in cooperatively breeding societies, raising the question of whether and how alloparenting may be activated by hormonal events in these females [24].

Allonursing, or the nursing of non-offspring infants, is physiologically costly to the female, but may provide allosuckled infants with increased growth, transferred immune compounds and improved survival rates [48,49]. In mammalian mothers, two hormones primarily control lactation: prolactin, which stimulates milk secretion, and oxytocin, which stimulates milk ejection [50]. Allolactators are frequently females who were recently pregnant but may have lost their own litters, suggesting that allonursing is also linked closely with the endocrinology of pregnancy [51]. Pseudopregnancy, which is particularly common in

canids, may likewise cause spontaneous lactation and thus allow for allonursing behavior [52,53]. However, it remains possible that allonursing may result from misdirected care or from milk theft, which may occur because group-living forces a female to rear her young in close proximity to others [17].

Both juvenile and adult males participate in alloparental behavior in a variety of mammalian species [54], yet relatively little is known about the role hormones play in the mediation of paternal and alloparental care in males [34,55]. Hormones similar to those influencing maternal behaviors might facilitate paternal behavior, namely testosterone, prolactin, and oxytocin [56]. However, the paucity of data on male alloparental hormones is further exacerbated by the confounding seasonal changes that most male mammals undergo during the breeding period, making it difficult to distinguish between hormonal changes driven by the environment versus by parental status [55].

Some experiments have been conducted to reveal the role of each hormone in terms of alloparental investment, particularly in rodents and primates (this issue); however, reports on larger mammals are extremely scarce and lack experimental support [55,57]. Even for cooperative breeders, most endocrine studies remain correlative, where increases or decreases in hormone levels are related to breeding status or periods of offspring dependence. Improving our understanding of the hormonal basis of alloparental behavior in a wide range of mammalian species, including carnivores, may clarify both the proximate and ultimate basis for cooperative breeding.

4. Literature review

We conducted a systematic literature review to investigate the endocrine basis of cooperative breeding in terrestrial members of the mammalian order Carnivora. Specifically, our goal was to synthesize knowledge of the hormones involved in reproductive suppression (including pseudopregnancy) and alloparental care in social carnivores. We first compiled a list of species exhibiting at least one form of alloparental care (e.g., cooperative defense, allonursing/alloprovisioning) from recent reviews of cooperative breeding and alloparental care [14,15]. Included in our initial list were: 1) all carnivore species categorized as either cooperative or communal breeders by Lukas and Clutton-Brock [15] and 2) all gregarious carnivore species exhibiting any form of alloparental care as in Isler and van Schaik [14]. This yielded 37 species, which belonged to the families Canidae (20 species), Eupleridae (1 species), Felidae (1 species), Herpestidae (6 species), Hyaenidae (3 species), Mustelidae (3 species), and Procyonidae (3 species; Table S1).

Using this list of 37 species, we performed a search in Google Scholar for the Latin name of each species and one of the seven classes of hormones identified in Saltzman [33] as a potential mediator of cooperative breeding and alloparental behavior (Table 1). Thus, our literature searches contained one Latin name and each one of the following hormone terms individually: “luteinizing hormone,” “androgen,” “testosterone,” “estrogen,” “estradiol,” “progesterone,” “progesterone,” “glucocorticoid,” “cortisol,” “prolactin,” and “oxytocin.” We then repeated each search by also adding the terms “cooperative breeding” or “alloparental care” in the search field for each pair of

candidate species and hormone. For example, for meerkats, we ran the following three separate queries for the hormone oxytocin: 1) “*Suricata suricatta*” “oxytocin”, 2) “*Suricata suricatta*” “oxytocin” “cooperative breeding” and 3) “*Suricata suricatta*” “oxytocin” “alloparental care”.

Of our original list of 37 species of carnivores with possible cooperative breeding and/or alloparental care (Table S1), we identified publications that contained data about these hormones for only 13 species. Of these, the bush dog (*Speothos venaticus*), European badger (*Meles meles*), maned wolf (*Chrysocyon brachyurus*), and spotted hyena (*Crocuta crocuta*) exhibit rare (if any) cases of allonursing and/or alloprovisioning behavior [58,59]. All four of these species were therefore excluded from this review.

In total, endocrine data relevant to cooperative breeding and alloparental care were only available for nine species of social carnivore. Our literature review yielded six canid species [coyote (*Canis latrans*), gray wolf (*C. lupus*), Ethiopian wolf (*C. simensis*), African wild dog, Arctic fox, red fox (*V. vulpes*)] and three herpestid species [meerkat, dwarf mongoose (*Helogale parvula*), banded mongoose] in which non-breeding adults regularly engaged in cooperative breeding, allonursing, and/or alloprovisioning. For each of these nine species, we first provide a brief overview of the cooperative breeding system as background to our discussion on the hormones mediating these behaviors (Table 2). Then, we quantify the hormone levels for breeders relative to non-breeders and for helpers relative to non-helpers in an effort to understand the extent to which each candidate hormone acts, on average, to suppress reproduction or promote alloparenting behavior across social carnivores (for details, see Tables S2 and S3).

5. Female reproductive suppression and pseudopregnancy

Reproductive suppression occurs in certain groups of social carnivores when a subset of sexually-mature females delay their age of first reproduction after puberty or fail to breed altogether [10]. Our review synthesizes the current knowledge about hormones involved in reproductive suppression and pseudopregnancy, as discussed below for the canid and herpestid families (Fig. 1, Table 3).

5.1. Canidae

As is true for most free-living carnivores, scientific knowledge regarding female reproductive physiology is limited in canids, primarily due to the difficulty of obtaining adequate sample sizes for analysis. As such, the majority of existing knowledge comes from captive studies, where a social group is arbitrarily created for cooperative breeders (Fig. 1, Table 3). Most of the studied canids share many reproductive attributes, including monoestrus cycles, long proestrus and luteal phases, behavioral suppression, and spontaneous ovulation with pseudopregnancy [37,60].

In the canid estrus cycle, estrogen concentrations typically increase during proestrus and decline during estrus regardless of pregnancy. Estrus begins with a surge in LH, after which progesterone rapidly rises. In pregnant female canids, progesterone remains elevated until parturition, and in pseudopregnant females progesterone remains elevated throughout an extended luteal phase approximating the length of

Table 1
Candidate hormones mediating reproductive suppression and alloparental care in mammals.

Hormone	Actions in breeders
Androgen (testosterone)	Sex steroid hormone; stimulates male secondary sexual characteristics and sperm production
Estrogen (estradiol)	Sex steroid hormone; regulates female reproductive cycles
Glucocorticoid (cortisol)	“Stress” steroid hormone; regulates energy balance, mediates “fight or flight” response and trade-offs in immune function and reproduction
Luteinizing hormone	Sex steroid hormone; triggers ovulation in females
Oxytocin	Peptide hormone; associated with lactation, pair-bonding and orgasm
Progesterone (progesterone)	Sex steroid hormone; supports pregnancy
Prolactin	Peptide hormone; supports pregnancy and stimulates milk production

Table 2
Biology of cooperatively breeding carnivores with endocrine data.^a

Family	Species	Breeding system	Group size	Reproductive skew	Helping behavior
Canidae (dogs)	Coyote (<i>Canis latrans</i>)	Monogamous pair bond (basic unit), but facultatively cooperative (may be joined by associates)	2–10 individuals	60–90% of females breed; 70% of yearlings produce litters	Pups are reared by breeding pair and associates (usually adult siblings)
	Gray wolf (<i>Canis lupus</i>)	Monogamous dominant pair bond (basic unit), but facultatively cooperative (often joined by offspring)	5–12 individuals (up to 36)	Dominant pair breeds, but other females suppressed unless food abundant	Den attendance and provisioning of food by helpers
	Ethiopian wolf (<i>Canis simensis</i>)	Obligate cooperative breeders living in multi-male philopatric packs comprised of daughters of alpha female	3–13 adults	Only 60% of females breed, but dominant female breeds every year	Helpers patrol, allonurse (50% of individuals exhibit pseudopregnancy), and provision pups
	African wild dog (<i>Lycan pictus</i>)	Obligate cooperative breeders with one dominant pair (basic unit) in pack	4–9 individuals (up to 30) adults and yearlings	One dominant breeding pair usually suppresses reproduction of others; subordinates may breed but are rarely successful	All pack members provision mothers and pups by regurgitating meat; babysitting and group defense also occurs
	Arctic fox (<i>Vulpes lagopus</i>)	Monogamous pair (basic unit), but may be communal (one to several closely related breeding pairs may share a den)	2–12 individuals (up to 18)	One dominant breeding pair usually suppresses reproduction of yearling females	Non-breeding yearlings help by provisioning young with meat
Herpestidae (mongooses)	Red fox (<i>Vulpes vulpes</i>)	Communal (one male shares den with two breeding females), pair bond (monogamous pair), or facultatively cooperative (breeding pair and several non-breeding related female helpers)	2–7 individuals	Female reproductive suppression varies with population size and food density, enforced via infanticide, harassment and fetal reabsorption	Non-breeding female helpers may feed, groom, and babysit pups; adoption occurs and females allonurse
	Dwarf mongoose (<i>Helogate parvula</i>)	Obligate cooperative breeders comprised of dominant breeding pair, their offspring and other adult males and females	8–9 individuals (up to 32)	High reproductive skew reinforced socially (via infanticide) and hormonally; plural breeding; dominant female produces 73% of litters	Subordinates (mainly females) babysit (carry, guard against conspecifics and predators), allonurse (via pseudopregnancy), provision, and groom pups
	Banded mongoose (<i>Mungos mungo</i>)	Obligate cooperative breeders in cohesive groups comprised of closely related adult males and females along with their immature offspring	9–28 individuals (typically 15, up to 75)	Dominant males breed most often and guard females; limited skew because all adult females breed synchronously	Helpers (mainly young non-breeding males, but also breeding females) babysit (carry, guard) and provision pups
	Meerkat (<i>Suricata suricatta</i>)	Obligate cooperative breeders (2–3 family units, including adult males, adult females, and young of the dominant breeding pair)	4–9 individuals (up to 49)	Dominant female produces 75% and dominant male produces 80% of litters; infanticide and evictions enforce female reproductive suppression	Non-breeding helpers babysit (carry, guard), allonurse, and provision pups

^a All information summarized from Wilson & Mittermeier [2].

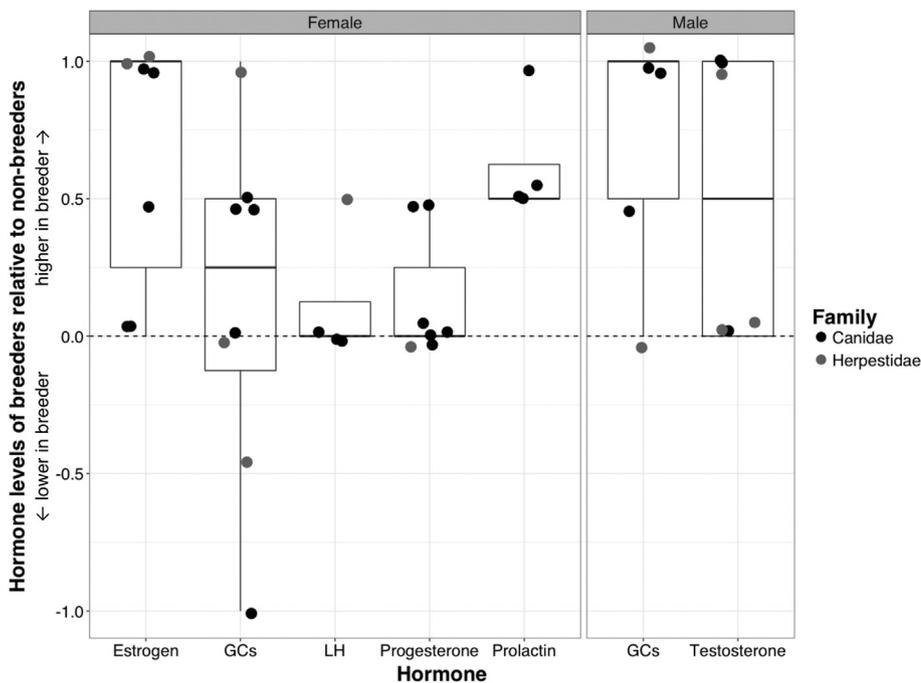


Fig. 1. Endocrine basis of reproductive suppression in carnivores. Box plots representing the extent to which breeding individuals in carnivore species belonging to Canidae (dog family) or Herpestidae (mongoose family) possess circulating levels of hormones that are, on average, relatively higher (indicated as a positive value), equivalent to (indicated as a zero value), or relatively lower (indicated as a negative value) than non-breeding members of that same species. Data points represent individual species. Data are available for estrogen, luteinizing hormone (LH), progesterone, and prolactin for females only and testosterone for males only. Glucocorticoid (GCs) data are available for both sexes.

gestation. High progesterone concentrations during the luteal phase are dependent on both LH and prolactin, both of which are also elevated [36]. Most wild canids appear to follow this general pattern of hormone secretion throughout the estrus cycle [37,61].

Studies of captive gray wolves reveal no hormonal differences between pregnant and pseudopregnant females, including LH, progesterone, and estrogen [29,62]. Thus, these studies find no evidence of physiological reproductive suppression in gray wolves, with most subordinate females exhibiting pregnancy or pseudopregnancy rather than failing to ovulate [29,62]. Studies of captive coyotes and African wild dogs provide similar results, with pregnant and pseudopregnant individuals showing no differences in estrogen or progesterone [35,60,63].

Results from captive studies of Arctic foxes and red foxes are similar to those from wolves and coyotes. At the beginning of estrus, foxes exhibit no differences in LH or progesterone based on breeding or dominance status [64–66]. In red foxes, progesterone concentrations remain similar between breeders and non-breeders throughout pregnancy [66]; in Arctic foxes, however, both estrogen and progesterone concentrations are higher in pregnant than non-pregnant females towards the end of gestation [67].

Unfortunately, it is impossible to know whether what is observed in captivity is also true in the wild, which makes studies of wild cooperatively breeding carnivores even more valuable. To our knowledge, researchers have investigated sex steroid hormones and reproductive suppression in wild populations of only two canid species: African wild dogs and Ethiopian wolves (Table 3).

Free-living female African wild dogs appear to exhibit some physiological reproductive suppression. Dominant females have significantly higher estrogen and progesterone concentrations during estrus than subordinates [68]; however, subdominant females do cycle and ovulate despite their lower estrogen concentrations [61]. It is likely that ovulation occurs in all female African wild dogs, but that behavioral suppression prevents copulation by subordinate females [61]; for example, lower estrogen concentrations may make subordinates less attractive to males and thus less likely to mate [11]. Ovulation without conception then results in a period of pseudopregnancy that likely increases rates of alloparenting behavior provided by subordinate females [61]. While allolactation and subsequent allonursing are rare in African wild dogs, subdominant females provision pups throughout the denning

period [68,69].

The reproductive physiology of Ethiopian wolves includes physiological suppression of subordinate females, and possible pseudopregnancy and allonursing of pups [70]. During the estrus cycle, significantly higher concentrations of estrogen are found in dominants than in subordinates, suggesting that subordinates are reproductively suppressed during the mating season [70]. Unlike in African wild dogs, estrus is observed during the mating season in all dominant females, but not in subordinate females, which further suggests that dominance status significantly affects a female's probability of coming into estrus [70]. However, dominant and subordinate females have indistinguishable progesterone concentrations during the dominant's pregnancy, suggesting that elevated progesterone and possibly pseudopregnancy promote allonursing by subordinates [37,70].

5.2. Herpestidae

Due to their smaller size, the herpestids have been well-studied in the wild, and they exhibit a range of patterns of reproductive suppression for adult females (Fig. 1, Table 3). In the banded mongoose, all subordinate females typically ovulate and breed, suggesting no difference in sex steroid levels due to status [31]. In the dwarf mongoose, baseline estrogen concentrations are higher in dominants than in subordinates, a difference magnified during estrus, when estrogen levels in dominants are more than triple that of their subordinates [28]. Estrogen levels remain elevated in dominants throughout pregnancy until parturition. Among subordinates, these low baseline levels of estrogen may lead to low mating rates by reducing their attractiveness as mates; for those who do manage to mate, the low estrogen concentrations during estrus could cause a failure to establish pregnancy [28]. Pseudopregnancy and spontaneous lactation can also occur in the dwarf mongoose, and are hormonally characterized by higher estrogen levels than in other non-pregnant, non-lactating individuals [52].

In meerkats, dominants appear to enforce reproductive suppression using aggression, and often temporary eviction from the group, to impose stressors upon subordinates. During their pregnancy, dominant females become more aggressive towards subordinate females, which increases GCs in subordinates during their dominant's pregnancy [45,71]. Pregnant dominant females also temporarily evict some subordinate individuals from the group; while evicted, these females

Table 3
Endocrine basis of reproductive suppression in adult female carnivores.

Species	Category	Luteinizing hormone	Estrogen	Progesterone	Prolactin	Glucocorticoids
Coyote (<i>Canis latrans</i>)	Breeder vs. non-breeder ^a	No differences [63]	No differences [63]	No differences [63]	No differences in first half of gestation, higher in pregnant females in second half of gestation [63]	No differences [29]; higher in dominants [81]
	Pregnant vs. non-pregnant ^b	Little difference [63]	Little difference [63]	No differences [63]	Higher in pregnant/lactating females (although all females exhibit seasonal increase) [95]	No differences [29]
Gray wolf (<i>Canis lupus</i>)	Breeder	No differences [62]	No differences [62]	No differences [29,62]		No differences [70]
	Pregnant vs. non-pregnant	No differences [62]	No differences [29,62]	No differences [29,62]		No differences [70]
Ethiopian wolf (<i>Canis simensis</i>)	Breeder vs. non-breeder	Higher in dominant females [70]	Higher in dominant females [70]	No differences (elevated in all females) [70]		Higher in dominant females [68]; no differences [82]
	Pregnant vs. non-pregnant	Higher in dominant females during estrus [68]	Higher in dominant females during estrus [68]	No differences between pregnant & pseudo-pregnant [35]		No differences between pregnant and pseudo-pregnant [82]
African wild dog (<i>Lycodon pictus</i>)	Breeder vs. non-breeder	Higher in dominant females during estrus [68]	Higher in dominant females during estrus [68]	Higher in pregnant females in second half of gestation [65,67]		Higher in pregnant females at end of gestation [67]
	Pregnant vs. non-pregnant	Higher in dominant females during estrus [68]	Higher in dominant females during estrus [68]	Little difference [66]	Higher in pregnant females in second half of gestation [66]	Lower in pregnant females [66]
Arctic fox (<i>Vulpes lagopus</i>)	Pregnant vs. non-pregnant	No differences [64]	Higher in pregnant females at end of gestation [67]	Higher in pregnant females in second half of gestation [65,67]		Higher in dominant females [83]
Red fox (<i>Vulpes vulpes</i>)	Pregnant vs. non-pregnant	No differences [66]	Higher in dominant females [28]	Higher in dominant females [28]		No differences prior to conception or in first trimester of gestation [85]
Dwarf mongoose (<i>Helogale parvula</i>)	Breeder vs. non-breeder	Higher in dominant females [28]	Higher in dominant females [28]	Higher in dominant females [28]		Lower in dominant females during second and third trimesters [85]
Banded mongoose (<i>Mungos mungo</i>)	Breeder vs. non-pregnant	Higher in dominant females [26,72–75]	Higher in dominant females [26,72–75]	No differences [75]		Higher in dominant females [72]; no differences [74,84]
Meerkat (<i>Suricata suricatta</i>)	Breeder vs. non-pregnant	Higher in dominant females [27]; no differences [72]	Higher in dominant females [26,72–75]	No differences [75]		No differences [84]; higher in subordinate females [71]

^a Breeder vs. non-breeder: hormone differences evaluated during the breeding season.

^b Pregnant vs. non-pregnant: hormone differences evaluated during the pregnancy period between cycling individuals.

Table 4
Endocrine basis of reproductive suppression in adult male carnivores.

Species ^a	Category	Testosterone	Glucocorticoids
Gray wolf (<i>Canis lupus</i>)	Breeder vs. non-breeder ^b	No differences [29]	Higher in dominant males [81]
Ethiopian wolf (<i>Canis simensis</i>)	Breeder vs. non-breeder	Higher in dominant males [78]	Higher in dominant males [78]
African wild dog (<i>Lycaon pictus</i>)	Breeder vs. non-breeder	Higher in dominant males during breeding season [35,68,76]	Higher in dominant males [68]; no differences [82]
Dwarf mongoose (<i>Helogale parvula</i>)	Breeder vs. non-breeder	No differences [28,79]	No differences [83]
Banded mongoose (<i>Mungos mungo</i>)	Breeder vs. non-breeder	Higher in dominant males during breeding season [77]	
Meerkat (<i>Suricata suricatta</i>)	Breeder vs. non-breeder	No differences [72,73,80]	Highest in dominant males, then natal subordinates, then immigrant subordinates [72]

^a No data were available for coyotes (*Canis latrans*), Arctic foxes (*Vulpes lagopus*), or red foxes (*Vulpes vulpes*) for either of the candidate hormones.

^b Breeder vs. non-breeder: hormone differences evaluated during the breeding season.

experience extremely high GC levels that cause downregulation of the reproductive system, including reduced conception and increased abortion rates [45]. Subordinate females also have generally lower baseline levels of LH and estrogen [26,27,72,73], which are not related to the temporary evictions nor attributed to any chronic stress of subordination [74]. Despite subordinates' lower baseline levels of reproductive hormones, recent work has demonstrated that all adult females regardless of rank possess adequate hormone levels for full-term pregnancies [75]. Reproductive suppression in meerkats therefore appears to be primarily the result of behavioral interference by the dominant female via eviction of pregnant subordinates or infanticide of subordinate pups [74,75]. Allonursing is far more common in meerkats than in dwarf mongooses, occurring in roughly 50% of litters [51].

6. Male reproductive suppression

In some carnivore species, male reproductive hormones are suppressed in subordinates (non-breeders) when in the presence of their dominants (breeders; Fig. 1, Table 4). For example, in both captive and wild African wild dogs, dominant males have significantly higher testosterone concentrations than subordinates during the mating season [35,68], suggesting that dominant males may be able to suppress their subordinates' testosterone levels [76]. In one study, although the dominant male had testosterone concentrations at least 20 times that of subordinates, subordinates and dominants had similar testicular volumes and sperm production during the mating season [76]; this is unusual in that elevated testosterone usually supports greater testes size and sperm production [34]. In banded mongooses, dominant males have higher testosterone concentrations than subordinates during the mating season, but not during the rest of the year [77]. In contrast, although dominant Ethiopian wolves have higher overall testosterone concentrations than subordinates, this difference is not significant during the mating season [78]. This indicates that subordinate male Ethiopian wolves are likely behaviorally suppressed, and observations suggest that subordinates are often prevented from mating by the dominant male [78].

Other carnivore species, however, show no rank- or breeding-related differences in testosterone levels (Fig. 1, Table 4); in species with high reproductive skew, reproduction is therefore behaviorally suppressed. Subordinate male gray wolves and dwarf mongooses have testosterone levels indistinguishable from those of dominants, but are prevented from mating by the dominant male [28,29,79]. Likewise, dominant and subordinate male meerkats have similar levels of both LH and testosterone [27,72,73,80]. In these species, failure to breed by reproductively mature males appears to be the result of direct behavioral interference by dominant males rather than endocrine deficiencies.

7. Stress-induced reproductive suppression

The effect of GCs on reproductive suppression in social carnivores appears to be sex-specific. In male carnivores, most of the data on stress hormones (Fig. 1, Table 4) support the 'stress of dominance' theory, which predicts that dominants have higher GC concentrations than subordinates. In canids, this theory is supported by cooperatively breeding gray wolves and Ethiopian wolves [78,81], although in African wild dogs the relationship between rank and GC levels is debated [68,82]. Similarly, in the herpestid family, dominant male meerkats have the highest GC concentrations, followed by natal subordinates, then immigrant subordinates [72], while no rank- or breeding-based differences are found in dwarf mongoose males [83].

In female carnivores, rank and breeding relationships with GCs are species-specific (Fig. 1, Table 3), and there is no clear pattern within either the canid or herpestid families. In free-living canids, dominant gray wolf females display higher GC levels with no decrease in fertility [81], while no difference in GCs is found between dominant and subordinate Ethiopian wolves [70]. In female African wild dogs, the relationship between rank and GC levels is again under debate [68,82]. For red foxes, GC levels are elevated in non-pregnant females, indicating a possible stress-related mechanism in their reproductive suppression [66]. In herpestids, subordinate female meerkats have higher GCs than dominants during their dominant's pregnancy or while temporarily evicted from the group [45,71]. Aside from these periods, however, dominant and subordinate female meerkats have similar GC levels [74,84]. Among banded mongooses, rank-related maternal stress during gestation leads to reduced reproductive success in subordinate females [85], although dominant dwarf mongoose females exhibit higher GC levels than subordinates without any apparent fertility costs [83].

8. Alloparental care

Studies of the endocrine basis of alloparental care are limited to only five carnivore species, with the great majority of work focusing on meerkats (Fig. 2, Table 5). Meerkats engage in many strictly alloparental behaviors, including babysitting, feeding, and teaching pups how to forage [26,86,87]. Peptide hormones such as prolactin and oxytocin, which are associated with parental care across vertebrates [46], likewise promote alloparental care in meerkats. Male meerkats who opt to remain at the nest and babysit on a given day have higher plasma levels of prolactin earlier in the day [88]. Increased prolactin is non-significantly associated with increased pup-feeding behavior [89], and peripheral administration of oxytocin also results in increased pup-feeding behavior and time spent associating with pups [90]. Gonadal steroids such as testosterone seem to have little effect on alloparental care in meerkats, including babysitting and pup-feeding [88,89],

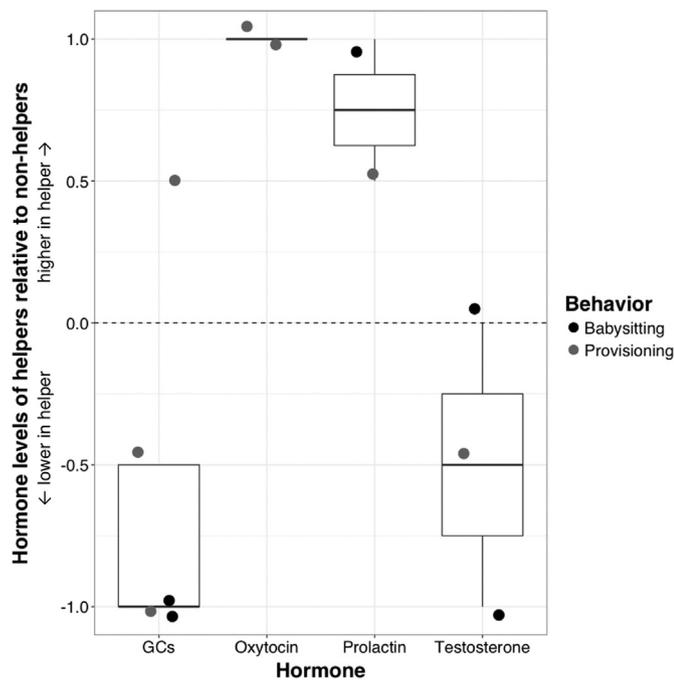


Fig. 2. Endocrine basis of alloparenting in carnivores. Box plots representing the extent to which individuals engaging in alloparental care (helpers) possess circulating levels of hormones that are, on average, relatively higher (indicated as a positive value), equivalent to (indicated as a zero value), or relatively lower (indicated as a negative value) than individuals who do not engage in alloparental care (non-helpers). All data come from Herpestidae (mongoose family) and include both sexes. Data points represent either males or females of a single species. Data are available for glucocorticoids (GCs), oxytocin, prolactin, and testosterone.

although a negative correlation between testosterone levels and pup-feeding rates exists in males during their extraterritorial prospecting periods [91]. In banded mongooses, high testosterone concentrations predict lower babysitting effort in the following days [77].

The association of alloparental behavior with GCs is more variable, even within a single carnivore species (Fig. 2, Table 5). In meerkats, individuals of both sexes who opt to remain at the nest and babysit have lower levels of GCs [88,92]. Although females with high GCs spend more time associating with pups [93], experimental manipulation of GCs shows that females with the lowest levels of GCs are more frequent in their pup-feeding behavior [92]. However, experimentally elevated levels of GCs increased the amount of provisioning by males [92]. Similarly, in naturalistic conditions, males with higher GC levels are more likely to participate in pup feeding [89]. In banded mongooses, however, males with low GC concentrations prior to the care period are more likely to provision pups [94]. There thus appears to be little consistency in the effects of GCs on alloparenting behavior, suggesting that other factors such as age, sex, and reproductive experience may be at play [92].

In canids, prolactin likely moderates alloparental behavior (Fig. 2, Table 5). However, there is little research that specifically disentangles alloparental care behavior from other temporal hormone and behavior changes in these seasonal breeders. Gray wolves of both sexes experience a rise in prolactin during the pup-rearing period, which could increase their alloparental input [95]. While all females regardless of pregnancy status experience this increase in prolactin, lactating wolf mothers exhibit the highest prolactin levels [95]. Likewise, in Arctic foxes, all females exhibit a seasonal increase in prolactin coinciding with lactation, although prolactin is highest in lactating mothers [64,96]. In coyotes and red foxes, however, prolactin rises significantly in pregnant and lactating females, but does not exhibit much change in non-pregnant individuals [63,66]. In addition to prolactin's effects in canid females, pseudopregnancy and the corresponding changes in sex

steroid hormones are thought to be a major component of the high levels of alloparental care (including allonursing) exhibited by subordinate females [37], although we could find no experimental evidence to support this.

9. Conclusion

Our study elucidates a strong bias towards endocrine research investigating mechanisms underlying reproductive suppression, but not alloparental care, within cooperatively breeding members of the order Carnivora. In general, our results show that breeding carnivores tend to have higher circulating levels of a suite of reproductive hormones than do non-breeders (Fig. 1, Tables 3 and 4). Breeding females typically have higher levels of estrogen, LH, progesterone, and/or prolactin than do other non-breeding adults, and breeding males often have elevated levels of testosterone compared to non-breeders. The effect of GCs on reproductive suppression in carnivores, however, appears to be sex-specific, as breeding males typically have higher GC levels than non-breeding subordinates, but females exhibit no clear trends in this relationship. These same reproductive and stress hormones control reproduction in other mammalian species, including primates and rodents [97,98], suggesting that a common group of hormones mediates the reproductive physiology of mammalian cooperative breeding. At low levels, these hormones likely act to suppress reproduction for non-breeding adults in cooperatively-breeding societies.

With respect to the endocrine basis of alloparental care in carnivores, we identify few published studies detailing the mechanisms shaping helping behaviors themselves, although these studies tend to follow the same general pattern observed in other mammals [46,99]. Overall, these studies indicate that elevated levels of prolactin and oxytocin, but reduced levels of testosterone and glucocorticoids, are associated with increased alloparental care (Fig. 2, Table 5). We could find no studies that investigated the effects of progesterone or estrogen on alloparental care in carnivores, although both hormones are thought to influence affiliative and cooperative behavior across mammals [57,100].

The patterns revealed here allow us to extend recent work investigating the endocrine basis of paternal care in carnivores [55]. Importantly, we echo de Bruin et al. [55] in emphasizing the skewed research focus in carnivore studies, which, despite a number of long-term studies [3], often lack endocrine data sufficient to address the issues explored in this review. We are surprised to see how few studies actually used fecal samples for their endocrine analysis, especially given recent advancements in non-invasive hormone monitoring [101,102]. Future work should utilize these non-invasive hormone sampling methods to fill these gaps in our knowledge and to identify the shared endocrine mechanisms promoting alloparental care in carnivores.

Whereas the evolutionary advantages of alloparental care have been extensively documented [10,13], our review reveals that the endocrine mechanisms mediating these behaviors have yet to be the subject of systematic study across cooperatively breeding species in the order Carnivora. Undoubtedly, this is a fruitful avenue for future studies, both for correlative research performed on free-living species and for experimental manipulations such as those conducted in meerkats [90,92]. Although we recognize the challenges associated with performing these endocrine studies in ecological contexts [103], there is also a need for studies investigating how hormonal mechanisms may mediate aspects of cooperative breeding beyond babysitting, allonursing, and alloprovisioning. Parallel investigations should thus aim to clarify the endocrine basis of group defense, predator detection, and communal denning in an effort to document the hormones promoting cooperation of all kinds in mammalian carnivores. Together, insights revealed here in combination with future avenues of inquiry are contributing to the emerging view that hormones play a central role in shaping the lives of social carnivores in particular and mammals in general.

Table 5
Endocrine basis of alloparental behaviors in both sexes of cooperatively breeding carnivores.

Species ^a	Sex	Testosterone	Prolactin	Oxytocin	Glucocorticoids
Gray wolf (<i>Canis lupus</i>)	Both		High prolactin during lactation period [95]		
Ethiopian wolf (<i>Canis simensis</i>)	Male	Does not decrease during denning [78]			
African wild dog (<i>Lycaon pictus</i>)	Male	Does not decrease during denning [68]			Does not vary within breeding period [82]
Arctic fox (<i>Vulpes lagopus</i>)	Female		Higher in lactating females, seasonal increase in all females coinciding with lactation [64]		
Banded mongoose (<i>Mungos mungo</i>)	Male	Males with low testosterone were more likely to babysit pups in following days [77]			Males with low cortisol prior to the care period were more likely to provision pups [94]
Meerkat (<i>Suricata suricatta</i>)	Male	No differences prior to choosing to babysit [88]; no differences prior to pup-feeding [89]; prospecting males had elevated levels of testosterone and reduced pup-feeding rates [91]	Higher in males prior to choosing to babysit [88]; no differences prior to pup-feeding in full model, but prolactin higher in males prior to pup-feeding without cortisol in model [89]		Lower in males prior to choosing to babysit [88]; higher in males prior to pup-feeding [89]; males with higher GCs exhibited increased pup-feeding [92] Females dosed with cortisol increased time spent close to pups [93]; females with lower GCs exhibited increased pup-feeding [92]
	Female			Individuals dosed with oxytocin were more generous in proportion of food fed to pups & spent more time close to pups [90]	Individuals dosed with cortisol showed no differences in pup feeding [93]; individuals dosed with mifepristone increased babysitting [92]

^a No data were available for coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), or dwarf mongooses (*Helogale parvula*) for any of the candidate hormones. No studies measured the effects of luteinizing hormone, estrogen or progesterone on alloparental care.

Declaration of interest

The authors declare that the review was written in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Appendix A. Supplementary tables

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