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A retrospective view of early research on dominance, stress and reproduction in cooperatively breeding carnivores☆

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ABSTRACT

Social carnivores have been central in studies of cooperative breeding, and research using noninvasive methods to examine behavioral and endocrine mechanisms of reproductive suppression started in the 1980s with dwarf mongooses in Serengeti National Park. Here, I synthesize the methods, findings and limitations of a research program that examined relationships between social dominance, age, mass, aggression, mating, gonadal steroids, glucocorticoids and reproduction in female and male dwarf mongooses, African wild dogs and wolves. Infanticide is a reliable backstop for reproductive suppression in females, and reproduction is energetically costly in these species. These conditions favor hypothalamic – pituitary – gonadal (HPG) adaptations that reduce the fertility of subordinate females to avoid the cost of producing doomed offspring. Infanticide also favors close synchronization of reproduction when subordinate females do become pregnant. In males, infanticide is a less reliable backstop and reproduction is less costly, so direct effects of subordination on fertility are less pronounced. Age is a strong predictor of social dominance in these species, but the evolutionary reason for this is not clear. In dwarf mongooses and wild dogs, alpha females were never deposed by younger packmates, but alpha males were: this difference is also not understood. Patterns of reproduction supported models predicting that alphas are less likely to share reproduction when the fitness costs of reproduction are high, when the fitness expected for dispersers is low, and with young subordinates to whom they are more closely related. Correlations between dominance and adrenal glucocorticoid concentrations varied between species and sexes, but did not support the hypothesis that chronic stress causes reproductive suppression.

In 1987, I began a study in Serengeti National Park of the ways that behavior, glucocorticoids and sex steroids related to social status in dwarf mongooses (*Helogale parvula*). The evolution of cooperative breeding had been a major focus of behavioral ecology since Hamilton's revolutionary theory of inclusive fitness (Hamilton, 1963, 1964a,b), and prior research had revealed a great deal about the demographic correlates and consequences of social dominance and subordination in dwarf mongooses (Rood, 1978, 1980, 1986, 1990). Jon Rood had found that large packs raised more offspring than small packs, that packs were mainly comprised of close relatives, that there was a clear (and relatively linear) dominance hierarchy within each sex, that few subordinate females became visibly pregnant, and that the alpha male defended access to the alpha female during mating periods. However, studies of the endocrine correlates of social status in wild populations were just beginning, and we knew nothing about the endocrine mechanisms that suppressed reproduction by subordinates. Why were social subordinates suppressed in some species like the dwarf mongoose, but not in ecologically and phylogenetically similar species like the banded mongoose (*Mungos mungo*) (Rood, 1975)? Was reproduction suppressed by chronic stress affecting the hypothalamic – pituitary – adrenal (HPA) axis (Christian and Davis, 1964; Sapolsky, 1982, 1985) or by more direct effects on the hypothalamic – pituitary – gonadal (HPG) axis (Reyer et al., 1986)? Were these mechanisms similar in males and females? Why and how did subordinates occasionally breed in species where reproductive suppression was the norm? Could we use evolutionary costs, benefits and constraints to understand differences between species and sexes in the mechanisms of reproductive suppression? These were the dominant questions, all virtually unstudied.

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Groundbreaking work by John Wingfield had established that endocrine processes could be studied in the wild by mist netting banded birds to collect blood samples, and this approach provided the first field study of reproductive suppression in a cooperative breeder, the Harris's sparrow (*Zonotrichia querula*) (Rohwer and Wingfield, 1981). Robert Sapolsky brought this approach to mammals by darting wild baboons, and found that subordinate males typically had higher circulating glucocorticoid concentrations and lower androgen concentrations than dominant males (Sapolsky, 1982, 1985), which aligned with data from captive rodents and primates (Creel, 2001). At the same time, biomedical and agricultural studies were developing non-invasive methods to measure urinary steroid hormone metabolites, which created the possibility for field studies of rank, aggression, endocrine function and reproduction without the stress of repeated capture, anesthesia and blood sampling (Erb et al., 1970; Shideler et al., 1983). At the same time, Lynn Carpenter devised a clever method to weigh birds without capture by converting a spring scale into a perch (Carpenter et al., 1983). Although this approach had not been applied to mammals, the potential was clear.

These were the starting points for early field studies of social behavior, glucocorticoids and reproduction in dwarf mongooses, African wild dogs (*Lycaon pictus*) and wolves (*Canis lupus*). Studies of captive callitrichid primates suggested that reproductive suppression of subordinates had an endocrine basis in females but might be purely behavioral in males (by preventing subordinates from mating with the fertile alpha female) (Abbott, 1984). As we noted 30 years ago, "reproductive suppression is often mediated by aggressive and agonistic interactions, [so] it is of particular interest to study the mechanisms of suppression in naturally assembled groups, where spacing patterns are free to vary and dispersal is freely available to subordinates" (Creel et al., 1992). This retrospective summarizes the questions that were central for these early studies, the approaches that were developed, the inferences that emerged, and the questions that remained.

1. Brief review of methods

The three studies all relied on observation of recognized individuals of known age and sex in the wild, coupled with non-invasive methods to collect urine or feces for measurement of steroid hormones or their metabolites (Fig. 1). The primary strengths of this approach are: (1) it describes hormone-behavior relationships as they operate in wild populations, (2) it allows many groups and individuals to be studied, and (3) it promotes integration of mechanistic studies with analysis of fitness costs and benefits. The primary weaknesses are: (1) it often does not include experimentation (to avoid affecting long term demographic data), (2) fecal and urinary steroid hormone metabolites provide noisy data that require extensive, representative sampling, (3) longitudinal hormone profiles for individuals are difficult to obtain, and (4) the patterns described are far from the binding of free steroids with their receptors (Love et al., 2004).

1.1. *Dwarf mongoose in Serengeti National Park*

In Serengeti National Park (Tanzania), we observed 179 individually recognized dwarf mongooses of known age and sex in eight packs living in an area of 25 km^2, from 1987 to 1990 (Creel et al., 1991, 1992, 1993; Keane et al., 1994; Creel et al., 1996). We used 1448 h of behavioral observation to describe patterns of aggression and social status. Of these, 393 h of observation fell within 71 mating periods (of 1–7 days), which we used to describe patterns of mating behavior and to test whether aggression changed during mating periods. We collected 740 urine samples from these individuals, which allowed radioimmunoassay (RIA) of urinary concentrations of estrogens, androgens and glucocorticoid conjugates. Assays were validated by standard tests for accuracy, precision, sensitivity and specificity, and by co-elution of immunoreactive metabolites with radiolabeled compounds in high pressure liquid chromatography. For glucocorticoids, we also confirmed a spike in response to trapping (Creel et al., 1997b). We collected 383 urine samples by capturing mongooses in box traps and placing a tray beneath

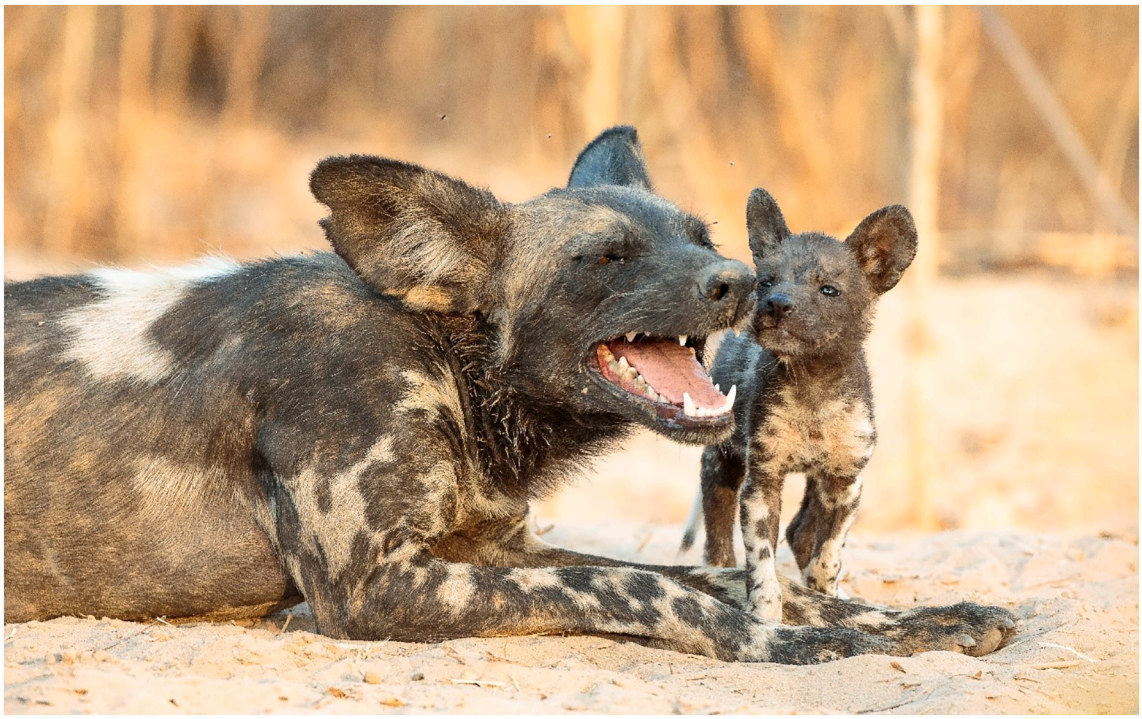

Fig. 1. Wild dogs, dwarf mongooses and wolves live in cooperative groups with reproduction largely monopolized by the dominant individual of each sex. Here, a non-breeding adult African wild dog attends to a pup at a den. Nonbreeding adults return to the den after hunting and regurgitate meat to the alpha female and her pups, who beg by nuzzling mouths and making a specific, birdlike 'yitter'.

the trap to collect urine, and 357 samples without capture, by taking advantage of the mongooses' propensity to scent mark with urine. For these, we placed a rubber pad near the group, retreated and watched until a mongoose urinated on it, recorded the animal's identity, collected the sample, cleaned the pad with water and replaced it. Negative controls confirmed that cross contamination did not affect our results. We also weighed mongooses 3016 times without capture, by setting out an electronic balance with a small cardboard and mesh enclosure mounted on it, watching until a single mongoose was on the scale, and recording its mass with binoculars or a spotting scope.

1.2. African wild dogs in the Selous Game Reserve

We studied social behavior, mating and endocrine function in African wild dogs in the Selous Game Reserve (Tanzania) from 1991 to 1996, observing an average of 105 individually-recognized individuals in up to nine packs in each year (Creel et al., 1996, 1997a; Creel and Creel, 2002). Wild dogs are individually recognizable from natural markings but they use huge territories, so we darted and radicollared one or two individuals per pack to allow relocation using very high frequency (VHF) telemetry. We observed packs (from a vehicle to which they habituated) for 2210 h during periods of activity around dawn and dusk, to record patterns of mating and aggression. We collected 247 fecal samples from 22 adult females and 34 adult males over a period of two years, by drawing a sketch map when a dog was observed to defecate, then collecting the scat at the end of the observation period. We extracted these samples for RIA of fecal testosterone, estrogen, progestin and glucocorticoid metabolites. These assays were validated using standard tests for accuracy, precision, sensitivity and specificity, longitudinal profiles of excretion and from three males (271 samples) and one female (188 samples) at the Brookfield zoo, recovery of radiolabeled estradiol and progesterone from the captive female (Monfort et al., 1997), and an adrenocorticotrophic hormone (ACTH) challenge (Monfort et al., 1998). For glucocorticoid metabolites, we also documented a short-term spike in response to darting and radiocollaring (Creel et al., 1997b). We initially planned to use a platform scale to collect data on body mass (as in the mongoose study), but concluded that it would require too much disturbance or habituation, which are both serious concerns with an endangered species.

1.3. Wolves in Yellowstone National Park

We studied social behavior, aggression and glucocorticoids in three packs of wolves in Yellowstone National Park (USA) in the winters of 1999 and 2000 (Sands and Creel, 2004). These packs held 7–8, 16–22 and 11–13 recognized wolves so that 35–40 animals were typically under study. At least four members of each pack carried a VHF radiocollar, which allowed us to observe wolves with a spotting scope, typically from distances greater than a kilometer. We observed behavior when packs were resting in open areas with good visibility for a total of 375 h. With the aid of range-finding binoculars we drew a sketch map whenever a wolf defecated, and waited until the pack had moved away to collect the scat (often on the following day). Because temperatures were usually well below freezing, most samples were frozen before we collected them. Because the distances from which we observed wolves were substantial, one observer remained at the point of observation and provided guidance by radio while another went to collect the scat. We collected 351 fecal samples, of which 124 were from known individuals in the three focal packs (or known lone wolves). We found the remaining samples when collecting scats we had observed. These additional samples were not useful for analyses that depend on knowing individual identity, but were useful to control for potentially confounding effects of scat composition, weather, season, and time of day. We quantified fecal glucocorticoid metabolites by immunoassay, validated with standard tests for sensitivity, precision, specificity and accuracy, and by an ACTH challenge with three captive wolves (Sands and Creel, 2004).

2. Summary of primary results

Table 1 summarizes the patterns we observed for social status and its determinants, behavior, gonadal steroids, adrenal glucocorticoids and reproductive success for females and males of the three species. In the sections that follow, I use these results to identify inferences, limitations and open questions, and to compare to results for other well-studied species.

3. Inferences with coherent support

3.1. Reproductive suppression in females and males

Vehrencamp (1983) laid out a framework that used inclusive fitness calculations to predict whether reproduction should be monopolized by a single individual (despotic societies) or shared among same-sexed pack mates (egalitarian societies). Vehrencamp's original model of reproductive skew assumed that the decision to monopolize or share reproduction is made by the dominant individual (a ‘concession’ model), though subsequent models have modified this assumption (‘tug-of-war’ models) (Keller and Reeve, 1994; Reeve and Keller, 2001). In general, reproductive skew models show that a high degree of reproductive skew (i.e., complete or near-complete reproductive suppression of social subordinates) should exist when: (1) Relatedness between dominants and subordinates is high. (2) Reproduction is energetically costly, so that assistance from groupmates appreciably increases the reproductive success of breeders, and producing a litter that is lost to infanticide appreciably reduces fitness. (3) The fitness expected for dispersers is low because local habitat is saturated with territorial groups (Emlen, 1982), dispersal is risky, or immigration into an existing group is difficult.

Our results and other studies (Keller and Reeve, 1994; Reeve and Keller, 2001; Abbot et al., 2011) suggest that all of these mechanisms help to predict the degree of reproductive suppression of social subordinates. In almost all species where subordinates typically do not breed, some subordinates do breed. Alphas are most likely to share reproduction with older subordinates, who are more distantly related because of breeder turnover (and thus accrue less indirect fitness by tolerating suppression and helping the alpha), and are more likely to become dominant if they disperse (and thus accrue more direct fitness if they do not remain in their current group) (Creel and Waser, 1991; Creel and Creel, 2002). These patterns are particularly clear for females (Creel and Waser, 1991, Creel and Creel, 2002), probably because alpha females have stronger control over reproduction than alpha males, and because reproduction carries particularly high energetic costs for females in these species.

To better understand whether alphas control the degree to which they share reproduction (and with whom), it is useful to recognize that infanticide is probably the original mechanism of reproductive suppression in evolutionarily primitive social groups. If an alpha can produce all the offspring that the group can raise and can identify whether offspring are its own, then selection will often favor killing subordinates' offspring (though any cost of overcoming resistance by subordinates must be considered). Most mammalian females can identify their own offspring under most conditions (particularly soon after birth), so infanticide can usually serve as a backstop if other mechanisms of reproductive suppression do not act first (Beehner and Lu, 2013). We very rarely observed infanticide, because it occurs soon after litters are born, while the offspring remain in an underground den. When subordinate females did produce litters, their birth was closely synchronized with the alpha female, usually on the same day in the same den, perhaps to reduce the certainty with which the alpha female could distinguish them (Creel et al., 1992; Creel and Creel, 2002). When a subordinate gave birth out of synchrony (even by just 1–2 days), the litter that emerged was typically no larger than alpha-only litters, reinforcing the inference (from genetic data) that infanticide is an effective backstop for other mechanism of reproductive suppression in females. Thus for

Table 1
Behavioral, endocrine and reproductive correlate of social status in female and male dwarf mongooses, African wild dogs and wolves.

	Dwarf mongoose		African wild dog		Gray wolf	
	Females	Males	Females	Males	Females	Males
Social organization						
Subordinates typically reproductively suppressed?	**Yes**, alphas comprised 22% of adult females but accounted for 73% (219 of 302) of pregnancies	**Yes**, alphas comprised 20% of adult male but accounted for 73% (415 of 566) of mating with alpha females	**Yes**, 82% of alpha females produce a litter annually, much greater than subordinate females (6%)	**Yes**, alphas comprised 16% of adult males but fathered 90% of offspring	**Yes**, pack structure is often simple, with only a breeding female and her nonbreeding offspring	**Likely**, mating with alpha female is primarily by alpha male
Subordinates sometimes reproduce?	**Yes**, 15% of offspring had subordinate mothers, particularly older females in larger packs. Share of maternity was less than share of matings by subordinates.	**Yes**, 24% of offspring had subordinate fathers, with multiple paternity within litters. Typically older males with low relatedness to the alpha. Share of paternity was similar to the share of matings by subordinates.	**Yes**, 6% of subordinate females produced litters and 8% of offspring had subordinate mothers. Share of maternity was less than share of matings by subordinates.	**Yes**, 10% of offspring had subordinate fathers, with shared paternity within litters. Share of paternity was similar to share of matings.	**Yes**. In the largest of 3 packs, three females simultaneously reproduced.	≈≈≈
Infanticide of subordinate's offspring when present?	**Yes**, joint litters (when one or more subordinates were pregnant) were larger than alpha-only litters, but the slope of offspring emerging vs. females pregnant was only 0.57 ± 0.20 (SE)	**No**, the share of paternity by subordinates (24%) was not detectably lower than their share of matings (27%). Shared paternity within litters would require clear phenotypic cues of paternity.	**Yes,** when subordinates reproduced even a few days out of synchrony with the alpha female, litters usually did not emerge. Infanticide by the alpha female has been directly observed.	**No**, alphas fathered 90% of offspring, similar to skew in patterns of mating (alpha males mated 5× more frequently than betas and 9× more often than males ranked third or below)	**Likely**, joint litters had fewer offspring/female	≈≈≈
Reproduction is energetically costly?	**Yes**, gestation cost of 159 kcal offspring/kg female mass$^{0.75}$ is more than twice that of banded mongoose. Litter growth during lactation of 17.9 g per day/kg female body mass$^{0.75}$ is greater than all social carnivores without reproductive suppression. Pairs without helpers rarely raise any offspring.	**Intermediate**. Males help to raise pups by teaching them to forage and defending them, but do not directly pay the exceptionally high costs of gestation and lactation.	**Yes**, with the costliest mammalian gestation on record, 308 kcal offspring/kg female mass$^{0.75}$. Lactation costs have not been measured but are clearly large. Pairs without helpers rarely raise any offspring.	**Intermediate**. Males help to raise pups by regurgitating meat and defending them, but do not directly pay the exceptionally high costs of gestation and lactation. Pups are given first access to kills once they can follow hunting groups.	**Yes**, gestation cost of 174 kcal offspring/kg female mass$^{0.75}$ is greater than in social carnivores without reproductive suppression. Litter growth rate of 67.3 g per day/kg female body mass$^{0.75}$ is notably rapid	**Intermediate/No**. Male provisioning of pups is much less extensive than in wild dogs
Behavior						
Determinants of rank	**Age** explains 69% of variance in rank, oldest dominant. **Body mass** explains 14% of variance	**Age** explains 69% of variance in rank, oldest dominant. **Body mass** explains 14% of variance	Within each pack, **oldest adult female invariably dominant**; all females >7 were alphas. No alpha female ever deposed by younger packmate	Rank **increased steadily to age 5 then steadily decreased**. Old alphas males often deposed by younger packmates.	**Oldest female typically dominant**; nuclear family group structure is common.	**Oldest male typically dominant**; nuclear family group structure is common.
Dominants more aggressive?	**Yes**, alpha females fight 2.0 times more often than subordinates	**Yes**, alpha males fight 2.7 times more often than subordinates	**No**	**No**	**No**	**No**
Changes in aggression at mating periods	Yes, aggression rate **decreased** at mating but still dominants > subordinates	Yes, aggression rate **decreased** at mating but still dominants > subordinates	**Yes**, aggression rate **decreased** at mating, more strongly in subordinates	**Yes**, aggression **rate decreased** at mating, more strongly in subordinates, Severity increased so that wounds were common. 60% of within-pack **alpha male depositions** occurred in brief mating periods	**Yes**, aggression rate **increased** at mating	**Yes**, aggression rate **increased** at mating
Dominants mate more?	**Yes**, alphas mate 65% more often	**Yes**, alphas mate 65% more often. This bias is reduced when pack members are scattered	**Yes**, alphas mate 10× more than betas and 30× more than lower ranks	**Yes**, alphas mate 5× more than betas and 9× more than lower ranks	**No**? Mating rates not detectably related to rank in data from one pack	≈≈≈
Association between ranks of mating pairs?	**Yes**, estrous synchrony is very tight; ranks of mating pairs are **strongly correlated**; 68% of mating with	**Yes**, estrous synchrony is very tight; ranks of mating pairs are **strongly correlated**; 68% of mating with	**Yes**, but ranks of mating pairs are **weakly correlated;** estrous synchrony is imperfect so typically	**Yes**, but ranks of mating pairs are **weakly correlated**; estrous synchrony is imperfect so typically	≈≈≈	≈≈≈

(*continued on next page*)

Table 1 (*continued*)

	Dwarf mongoose		African wild dog		Gray wolf	
	Females	Males	Females	Males	Females	Males
	alpha female was by alpha male	alpha female was by alpha male	only one mating female	only one mating female		
Adrenal glucocorticoids and rank						
Basal glucocorticoid concentration	Urinary cortisol **positively correlated with rank**, particularly high in alpha females	Urinary cortisol **uncorrelated with rank**	Fecal glucocorticoid metabolites, **Alpha > Subordinates** by 2×	Fecal glucocorticoid metabolites, **Alpha > Subordinates** by 25%	Fecal glucocorticoid metabolites, **Alpha > Subordinates**, 38% difference	Fecal glucocorticoid metabolites, **Alpha > Subordinates**, 38% difference
Glucocorticoid concentration in acute stress response	Urinary cortisol increased 4×; **Dominants > Subordinates**, despite higher basal CORT in dominant females	Urinary cortisol increased 5×; **Dominants < Subordinates**, suggesting compromised acute HPA response in dominants despite similar basal CORT	≈≈≈	≈≈≈	Fecal glucocorticoid metabolites **increased during mating periods** but **uncorrelated with individual aggression rate**	Fecal glucocorticoid metabolites **increased during mating periods** but **uncorrelated with individual aggression rate**
Gonadal steroids and rank						
During nonmating periods	Urinary estrogen conjugate concentrations low; **Dominants > Subordinates**	Urinary androgens **uncorrelated with rank; Dominants testis size > Subordinates**	Fecal estrogens low in nonmating. **Subordinates > Dominants** in estrogen concentrations and estrogen:progestin ratio	Fecal T **uncorrelated** with rank; trend for betas > alphas	≈≈≈	≈≈≈
During mating periods	Urinary estrogen conjugate concentration increased; **Dominants > Subordinates**	Urinary androgens **uncorrelated with rank**; androgens **did not change at mating periods**, but **decreased** (by a factor of 3) **when facing severe aggression** during immigration	Fecal estrogens increased; **Dominants > Subordinates** in estrogen concentrations	Fecal T **positively correlated** with rank; **increased in alphas** (+4%), but decreased in betas (−21%) and lower ranks (−33%); trend for beta > alphas	≈≈≈	≈≈≈
During gestation	Urinary estrogen conjugate concentration **elevated 70× in pregnant (usually alpha) females**, and in pseudopregnant subordinates who subsequently lactate and nurse alphas' offspring, but not most subordinates	≈≈≈	Fecal **progestins greatly elevated in pregnant (usually alpha)** females but not in most subordinates	≈≈≈	≈≈≈	≈≈≈

≈≈≈: No data.

subordinate females, selection should favor adaptations that avoid the costs of reproduction, because infanticide causes the expected fitness benefit to be small. This provides a coherent explanation for the observed mechanisms that block ovulation.

In contrast, dominant males usually cannot depend on infanticide to enforce reproductive suppression. When subordinate male mongooses or wild dogs reproduced, it was invariably because they fathered a fraction of the offspring in a litter fathered primarily by the alpha male (Keane et al., 1994; Creel and Creel, 2002). If an alpha male has heavily monopolized mating with the alpha female, then he has reliable information that his likelihood of paternity is greater than that of subordinates (Keane et al., 1994; Creel et al., 1997a), but he has no direct information to distinguish who fathered each pup within a litter. Given this, phenotypic cues to determine paternity would have to be quite reliable for an infanticidal alpha male to avoid accidentally killing his own offspring (particularly if the other potential fathers are closely related to the alpha male, as they usually are: Keane et al., 1994, Creel and Creel, 2002). Because infanticide is a weaker backstop for reproductive suppression in males than in females, selection is more likely to maintain fertility in subordinate males. This is particularly true because the energetic costs of reproduction are lower for males than for females, weakening selection to avoid them. This provides a coherent explanation why reproductive suppression is more likely to be purely behavioral in males than in females, even in nearly monomorphic species like the dwarf mongoose and wild dog.

A positive feedback loop is likely to reinforce the evolution of reproductive suppression in females of species like the dwarf mongoose and African wild dog. Once reproductive suppression begins, the presence of nonbreeding helpers allows the energy invested in gestation and lactation to increase (i.e., selection should favor alphas who make use of the expected contribution of helpers). In turn, as the costs of reproduction increase, selection on mechanisms to avoid these costs becomes stronger for subordinates. This provides a coherent explanation for the evolution of obligate cooperative breeding in species like the dwarf mongoose and African wild dog, where reproductive skew is high, unaided pairs are rare and unlikely to raise offspring, and the costs of gestation and lactation are high (Creel and Creel, 1991; Creel and Waser, 1991; Creel and Creel, 2002, 2015). This explanation is reinforced by comparison to social carnivores with more egalitarian reproduction like the lion (*Panthera leo*) or the spotted hyena (*Crocuta crocuta*), which

produce smaller litters that grow slowly (Creel and Creel, 1991), with energetic demands that can be met by a single female.

3.2. Rank, stress and reproduction

As discussed above, infanticide is probably the original mechanism of reproductive suppression in evolutionarily primitive social groups. If infanticide is common, then any mechanism by which subordinates could avoid the costs of reproduction should be favored (given that the expected fitness benefits of attempted reproduction are low) (Sapolsky, 1982, 1985). Because chronically elevated glucocorticoids can suppress reproduction, effects of subordination on glucocorticoid concentrations could be one such mechanism (Creel, 2001; Young et al., 2006). Although the data are highly variable, there is considerable evidence that chronically elevated glucocorticoids cause a wide range of physiological costs unrelated to reproduction (Munck et al., 1984; Romero and Wikelski, 2001; Bonier et al., 2009; Romero and Wingfield, 2016). Such costs should create a selection pressure favoring mechanisms that directly alter the HPG function of subordinates without mediation by glucocorticoids. Thus in societies where reproductive suppression is typical for most subordinates, it is not surprising to find non-glucocorticoid-mediated mechanisms (but see Young et al., 2006). This provides a coherent explanation for data showing that stress responses rarely drive reproductive suppression of subordinates. Instead, elevated glucocorticoids are often associated with high rank, suggesting that chronic elevation of glucocorticoids might be a cost that partially offsets other benefits (most notably high reproductive success) of social dominance (Creel et al., 1996).

In summary, many of the questions that dominated early field studies of reproductive suppression of subordinates in cooperatively breeding carnivores now have relatively clear answers. In females, social subordination usually has effects on sex steroid concentrations that reduce mating rates and (via feedback loops that affect pituitary function) play a role in blocking ovulation. As predicted by reproductive skew models, these effects of subordination on ovarian function are weaker in older and higher-ranking subordinate females. Evolutionary logic also predicts that effects on HPG function should be less likely in subordinate males, and as predicted, the effects of subordination on androgens in males are weaker and less consistent than effects on ovarian steroids in females. Finally, evolutionary logic suggests that direct mechanisms of reproductive suppression should replace stress-mediated mechanisms (if this produces the same reproductive outcome but avoids non-reproductive costs) and as predicted, glucocorticoids are not chronically elevated in social subordinates for many species of cooperative breeders where reproductive suppression is the rule.

4. Limitations, unanswered and emergent questions

Despite the progress just summarized, our work and many other studies over the past 35 years have found variation that makes it difficult to predict exactly what we would observe in an unstudied species. For example, ovarian steroid concentrations were affected by subordination in both dwarf mongooses and African wild dogs, but subordinate mongooses had lower estrogen concentrations than dominant females, while subordinate wild dogs had higher estrogen concentrations and higher estrogen:progestin ratios than dominant females. In male dwarf mongooses, androgen concentrations did not correlate with rank or increase during mating periods, but in male wild dogs, androgen concentrations correlated with rank and increased during mating periods (along with the likelihood of aggressive rank-reversals). Some variables showed a pattern of continuous correlation across ranks, others differed dichotomously between alphas and subordinates, and some were not affected by rank. Such differences can be explained retrospectively, but remain difficult to predict. This observation probably just reflects the fact that there are more ways to break a complicated mechanism than to keep it working. There are many ways to disrupt reproduction. If infanticide creates a selection pressure to avoid producing offspring that are not likely to live, then any allele that disrupts follicular growth, ovulation or implantation will be favored. Given this, it is not surprising that different alternatives arose in different species. The endocrine mechanisms that allow reproduction have considerable phylogenetic inertia, but the mechanisms that suppress reproduction probably have less. This point is particularly relevant for females, which have more complex reproductive physiology than males.

It is not obvious why age was such a strong determinant of dominance. In mongooses, the oldest individual of each sex within a pack was invariably dominant. This pattern always held, even if some of the animals within the pack were immigrants (raising an interesting question of how they assess age, even far beyond the age of reproductive maturity). In wild dogs, no female ever lost alpha status to a younger pack mate, but younger pack mates deposed many alpha males. For both species, calculations explain why suppressed subordinates provide help to the alpha (Creel and Waser, 1991, 1994; Creel and Creel, 2002), but do not explain why age determines which individuals win the contest for alpha status and breeding. It is also not obvious why this age convention was absolute for mongooses of both sexes and female wild dogs, but not male wild dogs.

Observational field studies have allowed us to describe the behavioral and endocrine consequences of subordination in the wild, but despite the strengths of such research, there are important limitations. The number of individuals under study is often large (e.g., 179 dwarf mongooses), but it is difficult to obtain a large number of samples from a given individual, so temporal patterns are hard to resolve, particularly at short time scales. Because repeated capture is both difficult and disruptive, non-invasive sampling is desirable, but capture increases the odds of sampling an individual of particular interest (for example to assess whether specific female is pregnant: Creel et al., 1991). In my research, sampling relied mainly on maximizing observation during periods that animals were likely to urinate or defecate, for example just before foraging. For wild dogs and wolves, sampling relied completely on such observation. Sampling hair, feathers or claws might provide alternatives for some species (Veronesi et al., 2015; Hansen et al., 2016).

A further limitation is that relative to circulating steroids, the process of excretion adds appreciable noise to the data (though urinary and especially fecal measurements also dampen short-term temporal variation in circulating steroid levels by pooling over the period of excretion). Fecal or urinary steroid metabolites provide a good tool to assess systematic differences in circulating hormone levels at time scales of a day or more, but cannot address mechanisms that involve variation in the ratio of free to bound steroids, receptor-mediated mechanisms, or the higher levels of control by peptide hormones of the HPA or HPG axes. I do not see any clear solution to the limitations of different methods, so research programs that combine methods should perhaps be more common.

Finally, it is difficult to establish the effect on fitness of a specific behavioral or endocrine difference between individuals (Munck et al., 1984; Bonier et al., 2009; Romero and Wingfield, 2016). In cooperatively breeding carnivores, individuals of high and low rank differ with respect to many behavioral and endocrine variables, most of which vary on short time scales. With observational data, it is difficult to make strong inferences about which of these phenotypic traits cause differences in reproduction or survival, though logic or temporal sequencing sometimes establishes the causation underlying a set of correlations. Research programs that combine observational and experimental approaches are likely to provide advances that integrate good description of behavioral and endocrine mechanisms in nature and strong causal inferences about effects on fitness (Love et al., 2004).

5. Comparison to other well studied cooperatively breeding mammals

Table 1 summarizes my research with three cooperatively breeding

carnivores. At the outset of this paper, I described the prior studies that motivated this work and the questions that it intended to address. The rows in Table 1 serve as a concrete guide to the variables and relationships on which we focused. Many excellent studies have now examined the same questions in other mammals, including naked mole rats (*Heterocephalus glaber*) (Bennett et al., 2018; Edwards et al., 2020; Buffenstein et al., 2021; Coen et al., 2021), tamarins, marmosets and other primates (Abbott et al., 2003; Beehner et al., 2006; Digby et al., 2006; Saltzman et al., 2009; Beehner and Lu, 2013), spotted hyenas (*Crocuta crocuta*) (Ilany et al., 2021; Holekamp et al., 1996; Brown et al., 2021), and meerkats (*Suricata suricatta*) (O'Riain et al., 2000; Young et al., 2006, 2008; Kutsukake and Clutton-Brock, 2006). While my intent is not to provide a comprehensive review, it is informative to consider what inferences are reinforced by comparison to these studies, what inferences differ, and what points emerge that were not addressed by the variables in Table 1.

Studies of cooperatively breeding primates reinforce the inference that the relationship between glucocorticoid concentrations and rank varies among species, and that differences in the relationship between aggression and rank help to explain this variation (Abbott et al., 2003). These studies also show that rank can affect glucocorticoid concentrations by altering access to social support and affiliative behavior, a hypothesis that we did not consider and is not mutually exclusive with the mechanisms we found. Primate studies also reinforce the role of infanticide as a backstop that promotes reproductive suppression at earlier stages (e.g. ovulation), particularly in females (Beehner et al., 2006; Beehner and Lu, 2013). As in Table 1, reproductive suppression in primates can be mediated by social interactions, but can also be mediated by poor access to food among subordinates (Tardif et al., 2005; Beehner and Lu, 2013), a hypothesis we did not consider. While we found that the high cost of gestation and lactation promotes reproductive suppression in social carnivores (Creel and Creel, 1991), we did not test whether subordination restricts an individual's ability to pay these costs. Among wild dogs, pups are given first access to carcasses (Estes and Goddard, 1967), but no effect of rank on feeding has been reported for adults, so this mechanism is probably weak. Dwarf mongooses move as a group when foraging (to improve anti-predator vigilance and share its costs (Rood, 1990)), but they capture prey items individually, so this mechanism is again probably weak.

The naked mole rat is unique among mammalian cooperative breeders in that subordinates are not only reproductive suppressed, but pre-pubertal (Buffenstein et al., 2021, Coen et al., 2021). They are also unique for their relatively closed colony structure and because studies in captivity can replicate the conditions of life in the wild better than is possible for most cooperatively breeding mammals. This has allowed an exceptionally comprehensive understanding of the mechanisms of reproductive suppression. Comparison of eusocial naked mole rats with solitary and monogamous rodents reveals differences in HPG function at all levels, originating with oxytocin, vasopressin and corticotrophin-releasing factor (CRF) systems within the nucleus accumbens, amygdala, bed nucleus of the stria terminalis and lateral septal nucleus, leading to attenuation of LH release in response to GnRH-1 (Coen et al., 2021). In addition, many subordinates had circulating concentrations of prolactin that would be classified as hyperprolactinaemic in humans (Bennett et al., 2018). This effect of rank on prolactin was not seen in eusocial Damaraland mole rats (*Fukomys damarensis*), reinforcing the point that we often see "a lack of evolutionary convergence in the proximate control" when comparing the fine mechanistic details of reproductive suppression across species (Bennett et al., 2018). Naked mole rats also confirm that suppression of HPG function in subordinates is not caused by chronic activation of the HPA axis, as dominants and subordinates had comparable levels of fecal and urinary cortisol (Edwards et al., 2020). Finally, naked mole rates reconfirm the pattern that "reproductive physiology shows a less profound suppression in males than in females" (Coen et al., 2021), although subordinates of both sexes had lower circulating gonadal steroid concentrations, and gametogenesis was affected in both sexes. Finally, most naked mole rats do not disperse from their natal colony (Buffenstein et al., 2021), a strong constraint on alternative strategies for subordinates that was probably important in the evolutionary transition to eusociality.

The meerkat shows striking parallels to dwarf mongooses, as predicted by their similar ecology and close phylogenetic relationship (Rood, 1986). In particular, infanticide is a backstop that drives reproductive suppression through altered HPG function, with stronger effects of rank on HPG function in females than in males (via downregulation of pituitary LH release in response to GnRH) (O'Riain et al., 2000; Young et al., 2008). As in dwarf mongooses, these HPG differences are not mediated by chronic elevation of glucocorticoids (Young et al., 2006). Unlike dwarf mongooses, dominant female meerkats often use aggression to evict older subordinate females (Kutsukake and Clutton-Brock, 2006). As in dwarf mongooses (Creel and Waser, 1991), pregnancy is more likely for old, high ranking female meerkats than for young, low ranking subordinates. Unlike dwarf mongooses, these old subordinates are likely to become the target of severe aggression from the alpha female, leading them to temporarily emigrate (Kutsukake and Clutton-Brock, 2006). With eviction, subordinate females' fecal glucocorticoid metabolite concentrations rise, pituitary LH release is downregulated, the probability of conception decreases and the probability of abortion increases (Young et al., 2006). Evicted subordinates experience a small loss of body mass, so loss of access to resources may play a role in reproductive suppression, but this effect is small relative to the concurrent rise in fecal glucocorticoid metabolites (Young et al., 2006). Eviction is not common in cooperatively breeding carnivores, and is more likely to evolve if a decrease in group size has relatively little effect on the reproductive success or survival of dominants.

Social subordinates are not reproductively suppressed in spotted hyenas, but detailed long term studies of dominance and its correlates extend several of the inferences above. Unusually for social carnivores, female rank is inherited, so that rank differences are primarily between entire matrilines (Ilany et al., 2021). High ranking females have greater reproductive success (Holekamp et al., 1996), at least partly due to better access to food as in some primates (Beehner and Lu, 2013). Infanticide is common, and is "driven by competition over social status among matrilines" (Brown et al., 2021), reinforcing the inference that infanticide is a precursor to other mechanisms of reproductive suppression that act at earlier stages.

6. Conclusions

In many cooperatively breeding carnivores, subordinates do not breed, and field studies have provided coherent answers to many of the original proximate and ultimate questions about reproductive suppression. These studies have consistently shown that inhibition of ovarian steroid secretion often accompanies reproductive suppression in females. In some species, lab studies have allowed effects on ovarian function to be traced up through each level of the HPG axis to effects of social status on specific brain nuclei, but no field studies have provided such data. Reproductive suppression of males is more likely to be mediated by behavior and less likely to be mediated by inhibited hypothalamic – pituitary – gonadal function, and infanticide underlies many of the differences between females and males. Reproductive suppression is usually not mediated by chronically elevated glucocorticoids.

This retrospective was intended to provide a concise summary of the questions that motivated early field studies of the behavioral and endocrine correlates of rank in cooperative breeders, the methods that were developed, and the inferences that emerged. Most of these inferences have proved to be a durable foundation for an increasingly complete understanding of the consequences of rank in complex societies. Prospectively, this example might also be of use as a reminder of the basic attributes of such research: (1) collecting long term data from known individuals in wild populations, (2) using methods that minimize

effects on the processes under study, (3) integrating data of many types (e.g., behavioral, endocrine, energetic, demographic, ecological), and (4) identifying questions that have not been resolved (or even asked), and finding methods to answer them.

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