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

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

19 **Keywords:** dominance, reproductive suppression, cooperative breeding, estrogen, androgen,
20 glucocorticoid, aggression, mating, infanticide

21
22 In 1987, I began a study in Serengeti National Park of the ways that behavior, glucocorticoids and sex
23 steroids related to social status in dwarf mongooses (*Helogale parvula*). The evolution of cooperative
24 breeding had been a major focus of behavioral ecology since Hamilton's revolutionary theory of
25 inclusive fitness (Hamilton 1963, 1964a, b), and prior research had revealed a great deal about the
26 demographic correlates and consequences of social dominance and subordination in dwarf mongooses
27 (Rood 1978, Rood 1980, Rood 1990). Jon Rood had found that large packs raised more offspring than
28 small packs, packs were mainly comprised of close relatives, there was a clear (and relatively linear)
29 dominance hierarchy within each sex, that few subordinates female became visibly pregnant, and that
30 the alpha male defended access to the alpha female during mating periods. However, studies of the
31 endocrine correlates of social status in wild populations were just beginning, and we knew nothing
32 about the endocrine mechanisms that suppressed reproduction by subordinates. Why were social
33 subordinates suppressed in some species like the dwarf mongoose, but not in ecologically and
34 phylogenetically similar species like the banded mongoose (*Mungos mungo*) (Rood 1975)? Was
35 reproduction suppressed by chronic stress affecting the HPA axis (Christian and Davis 1964, Sapolsky
36 1982, Sapolsky 1985) or by more direct effects on the HPG axis (Reyer et al. 1986)? Were these
37 mechanisms similar in males and females? Why and how did subordinates occasionally breed in species
38 where reproductive suppression was the norm? Could we use evolutionary costs, benefits and
39 constraints to understand differences between species and sexes in the mechanisms of reproductive
40 suppression? These were the dominant questions, all virtually unstudied.

41 Groundbreaking work by John Wingfield had established that endocrine processes could be
42 studied in the wild by mist netting banded birds to collect blood samples, and this approach provided
43 the first field study of reproductive suppression in a cooperative breeder, the Harris's sparrow
44 (*Zonotrichia querula*) (Rohwer and Wingfield 1981). Robert Sapolsky brought this approach to mammals

45 by darting wild baboons, and found that subordinate males typically had higher circulating
46 glucocorticoid concentrations and lower androgen concentrations than more aggressive dominant males
47 (Sapolsky 1982, Sapolsky 1985), which aligned with data from captive rodents and primates (Creel
48 2001). At the same time, biomedical and agricultural studies were developing non-invasive methods to
49 measure urinary steroid hormone metabolites, which created the possibility for field studies of rank,
50 aggression, endocrine function and reproduction without the stress of repeated capture, anesthesia and
51 bleeding (Erb et al. 1970, Shideler et al. 1983). At the same time, Lynn Carpenter devised a clever
52 method to weigh birds without capture by converting a spring scale into a perch (Carpenter et al. 1983).
53 Although this approach had not been applied to animals, the potential was clear.

54 These were the starting points for early field studies of social behavior, glucocorticoids and
55 reproduction in dwarf mongooses, African wild dogs (*Lycaon pictus*) and wolves (*Canis lupus*). Studies of
56 captive Callithricid primates suggested that reproductive suppression of subordinates had an endocrine
57 basis in females but might be purely behavioral in males (by preventing subordinates from mating with
58 the fertile alpha female) (Abbott 1984). As noted 30 years ago, “reproductive suppression is often
59 mediated by aggressive and agonistic interactions (Sapolsky 1985), [so] it is of particular interest to
60 study the mechanisms of suppression in naturally assembled groups, where spacing patterns are free to
61 vary and dispersal is freely available to subordinates” (Creel et al. 1992). This retrospective summarizes
62 the questions that were central for these early studies, the approaches that were developed, the
63 inferences that emerged, and the questions that remained.

64 **Brief review of methods**

65 The three studies all relied on observation of recognized individuals of known age and sex in the wild,
66 coupled with non-invasive methods to collect urine or feces for measurement of steroid hormone
67 metabolites (Figure 1). The primary strengths of this approach are: (1) it describes hormone-behavior

68 relationships as they operate in wild populations, (2) it allows many groups and individuals to be
69 studied, and (3) it promotes integration of mechanistic studies with analysis of fitness costs and
70 benefits. The primary weaknesses are: (1) it often does not include experimentation (to avoid affecting
71 long term demographic data), (2) fecal and urinary steroid hormone metabolites provide noisy data that
72 require extensive, representative sampling, (3) longitudinal hormone profiles for individuals are difficult
73 to obtain, and (4) the patterns described are far from the binding of free steroids with their receptors
74 (Love et al. 2004).

75 *Dwarf mongoose in Serengeti National Park*

76 In Serengeti National Park (Tanzania), we observed 179 individually recognized dwarf mongooses of
77 known age and sex in eight packs living in an area of 25 km², from 1987 to 1990 (Creel et al. 1991, Creel
78 et al. 1992, Creel et al. 1993, Keane et al. 1994, Creel et al. 1996). We used 1448 hours of behavioral
79 observation to describe patterns of aggression and social status. Of these, 393 hours of observation fell
80 within 71 mating periods (of 1-7 days), which we used to describe patterns mating behavior and to test
81 whether aggression changed during mating periods. We collected 740 urine samples from these
82 individuals, which allowed RIA of urinary concentrations of estrogens, androgens and glucocorticoid
83 conjugates. Assays were validated by standard tests for accuracy, precision, sensitivity and specificity,
84 and by co-elution of immunoreactive metabolites with radiolabeled compounds in high pressure liquid
85 chromatography. For glucocorticoids, we also confirmed a spike in response to trapping (Creel et al.
86 1997b). We collected 383 urine samples by capturing mongooses in box traps and placing a tray
87 beneath the trap to collect urine, and 357 samples without capture, by taking advantage of the
88 mongooses' propensity to scent mark with urine. For these, we placed a rubber pad near the group,
89 retreated and watched until a mongoose urinated on it, recorded the animal's identity, collected the
90 sample, cleaned the pad with water and replaced it. Negative controls confirmed that cross
91 contamination did not affect our results. We also weighed mongooses 3,016 times without capture, by

92 setting out an electronic balance with a small cardboard and mesh enclosure mounted on it, watching
93 until a single mongoose was on the scale, and recording its mass with binoculars or a spotting scope.

94 *African wild dogs in the Selous Game Reserve*

95 We studied social behavior, mating and endocrine function in African wild dogs in the Selous Game
96 Reserve (Tanzania) from 1991 to 1996, observing an average of 105 individually-recognized individuals in
97 up to nine packs in each year (Creel et al. 1996, Creel et al. 1997a, Creel and Creel 2002). Wild dogs are
98 individually recognizable from natural markings but they use huge territories, so we darted and
99 radiocollared one or two individuals per pack to allow relocation using VHF telemetry. We observed
100 packs (from a vehicle to which they habituated) for 2,210 hours during periods of activity around dawn
101 and dusk, to record patterns of mating and aggression. We collected 247 fecal samples from 22 adult
102 females and 34 adult males over a period of two years, by drawing a sketch map when a dog was
103 observed to defecate, then collecting the scat at the end of the observation period. We extracted these
104 samples for RIA of fecal testosterone, estrogen, progesterin and glucocorticoid metabolites. These assays
105 were validated using standard tests for accuracy, precision, sensitivity and specificity, longitudinal
106 profiles of excretion and from three males (271 samples) and one female (188 samples) at the
107 Brookfield zoo, recovery of radiolabeled estradiol and progesterone from the captive female (Monfort et
108 al. 1997), and an ACTH challenge (Monfort et al. 1998). For glucocorticoid metabolites, we also
109 documented a short term spike in response to darting and radiocollaring (Creel et al. 1997b). We
110 initially planned to use a platform scale to collect data on body mass (as in the mongoose study), but
111 concluded that it would require too much disturbance or habituation, which are both serious concerns
112 with an endangered species.

113

114

115 *Wolves in Yellowstone National Park*

116 We studied social behavior, aggression and glucocorticoids in three packs of wolves in Yellowstone
117 National Park (USA) in the winters of 1999 and 2000 (Sands and Creel 2004). These packs held 7 - 8, 16 -
118 22 and 11 – 13 recognized wolves so that 35-40 animals were typically under study. At least four
119 members of each pack carried a VHF radiocollar, which allowed us to observe wolves using a spotting
120 scope, typically from distances greater than a kilometer. We observed behavior when packs were
121 resting in open areas with good visibility for a total of 375 hours. With the aid of range-finding
122 binoculars we drew a sketch map whenever a wolf defecated, and waited until the pack had moved
123 away to collect the scat (often on the following day). Because temperatures were usually well below
124 freezing, most samples were frozen before we collected them. Because the distances from which we
125 observed wolves were substantial, one observer remained at the point of observation and provided
126 guidance by radio while another went to collect the scat. We collected 351 fecal samples, of which 124
127 were from known individuals in the three focal packs (or known lone wolves). We found the remaining
128 samples when collecting scats we had observed. These additional samples were not useful for analyses
129 that depend on knowing individual identity, but were useful to control for potentially confounding
130 effects of scat composition, weather, season, and time of day. We quantified fecal glucocorticoid
131 metabolites by RIA, validated with standard tests for sensitivity, precision, specificity and accuracy, and
132 by an ACTH challenge with three captive wolves (Sands and Creel 2004).

133 **Summary of primary results**

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

137

138 **Inferences with coherent support**

139 *Egalitarian and despotic societies, females and males*

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

152 Our results and other studies (Keller and Reeve 1994, Reeve and Keller 2001, Abbot et al. 2011)
153 suggest that all of these mechanisms help to predict the degree of reproductive suppression of social
154 subordinates. In almost all species where subordinates typically do not breed, some subordinates do
155 breed. Alphas are most likely to share reproduction with older subordinates, who are more distantly
156 related (and thus accrue less indirect fitness by tolerating suppression and helping the alpha), and are
157 more likely to become dominant if they disperse (and thus accrue more direct fitness if they do not
158 remain in their current group) (Creel and Waser 1991, Creel and Creel 2002). These results were
159 particularly clear for female dwarf mongooses (Creel and Waser 1991) and African wild dogs (Creel and
160 Creel 2002), probably because the assumption that the decision to share reproduction is controlled by

161 the alpha is more closely met in females than in males, and reproduction carries particularly high
162 energetic costs for females of these species.

163 To better understand whether alphas control the degree to which they share reproduction (and
164 with whom), it is useful to recognize that infanticide is probably the original mechanism of reproductive
165 suppression in evolutionarily primitive social groups. If an alpha can produce all the offspring that the
166 group can raise and can identify whether offspring are its own, then selection will often favor killing
167 subordinates' offspring (though any cost of overcoming resistance by subordinates must be considered).
168 Mammalian females can identify their own offspring under most conditions, so infanticide can usually
169 serve as a backstop if other mechanisms of reproductive suppression do not act first. We very rarely
170 observed infanticide, because it occurs soon after litters are born, while the pups remain in the den at
171 all times. When subordinate females did produce litters, their birth was closely synchronized with the
172 alpha female, usually on the same day in the same den, probably to reduce the certainty with which the
173 alpha female could distinguish them (Creel et al. 1992, Creel and Creel 2002). When a subordinate gave
174 birth out of synchrony (even by just 1-2 days), the litter that emerged was typically no larger than alpha-
175 only litters, reinforcing the inference that infanticide is an effective backstop for other mechanism of
176 reproductive suppression in females. Thus for subordinate females, selection should favor adaptations
177 that avoid the costs of reproduction, if infanticide causes the expected fitness benefit to be small. This
178 provides a coherent explanation for the observed effects of social subordination on ovarian function in
179 dwarf mongooses and African wild dogs, which appear to block ovulation.

180 In contrast, dominant males usually cannot depend on infanticide to enforce reproductive
181 suppression. When subordinate male mongooses or wild dogs reproduced, it was invariably because
182 they fathered a fraction of the offspring in a litter fathered primarily by the alpha male (Keane et al.
183 1994, Creel and Creel 2002). If an alpha male has heavily monopolized mating with the alpha female,
184 then he has reliable information that his likelihood of paternity is much greater than that of a

185 subordinate male (Keane et al. 1994, Creel et al. 1997a), but he has no direct information to distinguish
186 who fathered each pup within a litter. Given this, phenotypic cues to determine paternity would have to
187 be quite reliable for an infanticidal alpha male to avoid accidentally killing his own offspring (particularly
188 if the other potential fathers are closely related to the alpha male, as they usually are: Keane et al. 1994,
189 Creel and Creel 2002). Consequently, infanticide is a weaker backstop for reproductive suppression in
190 males than in females, and selection is more likely to maintain fertility in subordinate males. This is
191 particularly true because the energetic costs of reproduction are lower for males than for females,
192 weakening selection to avoid them. This provides a coherent explanation why reproductive suppression
193 is more likely to be purely behavioral in males than in females, even in nearly monomorphic species like
194 the dwarf mongoose and wild dog.

195 A positive feedback loop is likely to reinforce the evolution of reproductive suppression in
196 females of species like the dwarf mongoose and African wild dog. Once reproductive suppression
197 begins, the presence of nonbreeding helpers allows the energy invested in gestation and lactation to
198 increase (i.e., selection should favor alphas who make use of the expected contribution of helpers). In
199 turn, as the costs of reproduction increase, selection on mechanisms to avoid these costs becomes
200 stronger for subordinates. This provides a coherent explanation for obligate cooperative breeding in
201 species like the dwarf mongoose and African wild dog, where reproductive skew is high, unaided pairs
202 are rare and unlikely to raise offspring, and the costs of gestation and lactation are high (Creel and Creel
203 1991, Creel and Waser 1991, Creel and Creel 2002, Creel and Creel 2015). This explanation is reinforced
204 by comparison to social carnivores with more egalitarian reproduction like the lion (*Panthera leo*) or the
205 spotted hyena (*Crocuta crocuta*), which produce smaller litters that grow slowly (Creel and Creel 1991),
206 with energetic demands that can be met by a single female.

207

208 *Rank, stress and reproduction*

209 As discussed above, infanticide is probably the original mechanism of reproductive suppression in
210 evolutionarily primitive social groups. If infanticide is common, then glucocorticoid-mediated
211 reproductive suppression is a plausible mechanism by which subordinates could avoid the costs of
212 reproduction (given that the expected fitness benefits of attempted reproduction are low) (Sapolsky
213 1982, Sapolsky 1985). Although the data are highly variable, there is considerable evidence that
214 chronically elevated glucocorticoids cause a range of physiological costs unrelated to reproduction
215 (Munck et al. 1984, Romero and Wikelski 2001, Bonier et al. 2009, Romero and Wingfield 2016). Such
216 costs should create a selection pressure favoring mechanisms that directly alter the HPG function of
217 subordinates without mediation by glucocorticoids. Thus in societies where reproductive suppression is
218 typical for most subordinates, it is not surprising to find non-glucocorticoid-mediated mechanisms. This
219 provides a coherent explanation for data showing that stress responses rarely drive reproductive
220 suppression of subordinates. Instead, elevated glucocorticoids are often associated with high rank,
221 suggesting that social stress might be a cost that partially offsets other benefits (most notably high
222 reproductive success) (Creel et al. 1996).

223 In summary, many of the questions that dominated early field studies of reproductive
224 suppression of subordinates in cooperatively breeding species now have relatively clear answers. In
225 females, social subordination usually has effects on sex steroid concentrations that reduce mating rates
226 and typically block ovulation. As predicted by reproductive skew models, these effects of subordination
227 on ovarian function are weaker in older and higher-ranking subordinate females. Evolutionary logic also
228 predicts that effects on HPG function should be less likely in subordinate males, and as predicted, the
229 effects of subordination on androgens in males are weaker and less consistent than effects on ovarian
230 steroids in females. Finally, evolutionary logic suggests that direct mechanisms of reproductive
231 suppression should replace stress-mediated mechanisms (if this produces the same reproductive

232 outcome but avoids non-reproductive costs) and as predicted, glucocorticoids are not chronically
233 elevated in social subordinates for many species of cooperative breeders where reproductive
234 suppression is the rule.

235 **Limitations, unanswered and emergent questions**

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

253 In mongooses, the oldest individual of each sex within a pack was invariably dominant. This
254 pattern always held, even if some of the animals within the pack were immigrants (raising an interesting

255 question of how they assess relative age, even for animals far beyond the age of reproductive maturity).
256 In wild dogs, no female ever lost alpha status to a younger pack mate, but younger pack mates deposed
257 many alpha males. It is not obvious why age is such a strong determinant of status, even though
258 subordination leads to reproductive suppression. Inclusive fitness calculations explain why suppressed
259 subordinates provide help to the alpha, but do not explain why age determines which individuals win
260 the contest for alpha status and breeding. It is also not obvious why this age convention was absolute
261 for mongooses of both sexes and female wild dogs, but not male wild dogs.

262 Observational field studies have allowed us to describe the behavioral and endocrine
263 consequences of subordination in the wild, but despite the strengths of such research, there are
264 important limitations. The number of individuals under study is often large (*e.g.*, 179 dwarf
265 mongooses), but it is difficult to obtain a large number of samples from a given individual, so temporal
266 patterns are hard to resolve, particularly at short time scales. Because repeated capture is both difficult
267 and disruptive, non-invasive sampling is desirable, but capture increases the odds of sampling an
268 individual of particular interest (for example to assess whether female is pregnant: Creel et al. 1991).
269 Because there is only alpha in each group, we tried to sample alphas at higher rates than subordinates,
270 but old, high ranking mongooses quickly learned to avoid traps by waiting and watching younger pack
271 mates. This required us to put out baited traps with their doors wired open for several days, so that the
272 mongooses would not be caught and lose their fear. During these pre-baiting sessions, old adults
273 watched others, observed that the traps were not closing, and only then entered traps. After several
274 days of pre-baiting we would set the traps, but old, high-ranking adults watched the younger animals,
275 saw that the traps were operating and avoided them. We then began wiring the doors open on most of
276 the traps but setting a few, with a small stick tied to fishing line running to the vehicle, so that
277 mongooses could come and go from the trap until we tripped it. Old mongooses would see less
278 cautious pack mates enter and leave such traps, and eventually went in, but this typically worked only

279 once. Such problems made it difficult to obtain samples from specific individuals in a specific time
280 window. Targeted sampling relied mainly on maximizing observation during periods that animals were
281 likely to urinate or defecate, particularly during social rallies just before foraging. For wild dogs and
282 wolves, sampling relied completely on such observation. Representative sampling of many individuals is
283 possible with urinary or fecal samples, but intensive longitudinal sampling of a given individual is difficult
284 and rarely accomplished. Sampling hair, feathers or claws might provide alternatives for some species
285 (Veronesi et al. 2015, Hansen et al. 2016).

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

294 Another problem (not unique to noninvasive sampling) is that it is difficult to establish the effect
295 on fitness of a specific behavioral or endocrine difference between individuals. This problem is well
296 recognized in research on the fitness effects of glucocorticoids (Munck et al. 1984, Bonier et al. 2009,
297 Romero and Wingfield 2016), but it pertains to other endocrine and behavioral mechanisms. In
298 cooperatively breeding carnivores, individuals of high and low rank differ with respect to many
299 behavioral, endocrine and demographic variables, most of which vary on short (and different) time
300 scales. With observational data, it is difficult to make strong inferences about which of these
301 phenotypic traits cause differences in reproduction or survival, though logic or temporal sequencing
302 sometimes establishes the causation underlying a set of correlations. Research programs that combine

303 observational and experimental approaches are likely to provide advances that integrate good
304 description of behavioral and endocrine mechanisms in nature and strong causal inferences about
305 effects on fitness (Love et al. 2004). Both approaches remain important, and the considerable variation
306 among species (*e.g.*, Table 1) leaves a lot of scope for a more general understanding of the effects of
307 social status on stress and reproduction.

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Figure 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'.

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 5X more frequently than betas and 9X more often than males ranked third or below)	Likely , joint litters had fewer offspring/female	≈≈≈
Reproduction is energetically costly?	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 teaching them to forage and defending them, but do not directly pay the exceptionally high costs of gestation and lactation.	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 grams 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 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 grams 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

	Dwarf mongoose		African wild dog		Gray wolf	
	Females	Males	Females	Males	Females	Males
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 10X more than betas and 30X more than lower ranks	Yes , alphas mate 5X more than betas and 9X 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 alpha female was by alpha male	Yes , estrous synchrony is very tight; ranks of mating pairs are strongly correlated ; 68% of mating with alpha female was by alpha male	Yes , but ranks of mating pairs are weakly correlated ; estrous synchrony is imperfect so typically only one mating female	Yes , but ranks of mating pairs are weakly correlated ; estrous synchrony is imperfect so typically only one mating female	≈≈≈	≈≈≈

	Dwarf mongoose		African wild dog		Gray wolf	
	Females	Males	Females	Males	Females	Males
Adrenal glucocorticoids and rank						
<i>Basal glucocorticoid concentration</i>	Urinary cortisol positively correlated with rank , particularly high in alpha females	Urinary cortisol uncorrelated with rank	Fecal glucocorticoid metabolites, Alpha > Subordinates by 2X	Fecal glucocorticoid metabolites, Alpha > Subordinates by 25%	Fecal glucocorticoid metabolites, Alpha > Subordinates , 38% difference	Fecal glucocorticoid metabolites, Alpha > Subordinates , 38% difference
<i>Glucocorticoid concentration in acute stress response</i>	Urinary cortisol increased 4X; Dominants > Subordinates , despite higher basal CORT in dominant females	Urinary cortisol increased 5X; 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						
<i>During nonmating periods</i>	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:progesterin ratio	Fecal T uncorrelated with rank; trend for betas > alphas	≈≈≈	≈≈≈
<i>During mating periods</i>	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	≈≈≈	≈≈≈
<i>During gestation</i>	Urinary estrogen conjugate concentration elevated 70X 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	≈≈≈	≈≈≈	≈≈≈