The interplay between social rank, physiological constraints and investment in courtship in male spotted hyenas

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Abstract
1. In many animal societies, dominant males have a higher reproductive success than subordinate males. The proximate mechanisms by which social rank influences reproductive success are poorly understood. One prominent hypothesis posits that rank-related male attributes of attractiveness and fighting ability are the main mediators of reproductive skew. Yet, empirical evidence in support of this hypothesis is limited. An alternative hypothesis emphasises the inherent social dimension of dominance relationships and posits that the relationship between male social rank and reproductive success is mediated by the physiological costs of male–male competition. This has not been tested in systems in which the two hypotheses can be disentangled.

2. We investigated the interplay between male social rank, physiological costs and male investment in social and sexual activities. We used measurements of faecal glucocorticoid metabolite concentrations (fGMC) as biomarkers of physiological costs and long-term behavioural data of 319 males in free-ranging spotted hyenas Crocuta crocuta, a species in which male access to females and reproductive success do not depend on physical attributes.

3. When males courted females and interacted with male competitors, low-ranking males had higher fGMC than high-ranking males. In contrast, fGMC did not vary with social rank when males were alone or when they courted females and competitors were absent. Low-ranking males minimised their exposure to physiologically costly intrasexual competition; they spent more time alone and less time engaging in social and sexual activities than did high-ranking males. They also invested less than high-ranking males in courting the most contested and highest-quality females.

4. Our findings demonstrate that the physiological costs of intrasexual competition in male spotted hyenas vary with social rank and shape behavioural trade-offs between the allocation of time and physiological resources to social integration, reproduction and self-maintenance. Our study suggests that physiological and social constraints play a pivotal role in the emergence of rank-related male reproductive success. The study provides insights into how the social organisation and breeding system shape physiological constraints and patterns of reproductive skew within and between species.

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1 | INTRODUCTION

In many group-living species in which societies are structured by social hierarchies, social rank positively correlates with reproductive success, with individuals of high rank producing more offspring and/or offspring of higher quality than those of lower rank (Cowlishaw & Dunbar, 1991; Ellis, 1995; Keller & Reeve, 1994). Extensive effort has been put into investigating how natural and sexual selection act on rank-related traits (Andersson, 1994; Clutton-Brock, 2007) and identifying the causes of variation in reproductive skew within and between species (Alberts, 2012; Ellis, 1995; Gogarten & Koenig, 2013; Keller & Reeve, 1994; van Noordwijk & van Schaik, 2004). Yet the proximate mechanism by which male social rank influences male reproductive success remains poorly understood (Alberts et al., 2003; Young et al., 2006).

Sexual selection theory predicts that, in males, reproductive success is primarily determined by the number of receptive females and the reproductive performance of the males, that is, their ability to access mates and create breeding opportunities (Andersson, 1994). Most theoretical and empirical models of reproductive skew are based on the premise that dominant males are more attractive to potential mates and/or more competitive than subordinate males because of superior intrinsic attributes (e.g. brighter plumage colour, larger body size, stronger weaponry, higher aggressiveness; Alberts et al., 2003; Cant & Reeve, 2002; Ellis, 1995; Port & Cant, 2014). In multimale, multifemale societies, (a) high-ranking males are therefore predicted to benefit from preferential access to mating partners—either via female mate choice or direct competitive exclusion of rivals—and sire the largest number of offspring in the group, and (b) male reproductive success is predicted to correlate with male rank order and associated quality of individual attributes. However, the findings of numerous empirical studies are inconsistent with these predictions; the investment in courtship and reproductive success of top-ranking males usually decrease when the number of competitors increases while the success of lower-ranking males increases (Alberts, 2012; Alberts et al., 2003; Cowlishaw & Dunbar, 1991; Dubuc et al., 2011; Gogarten & Koenig, 2013). These results suggest that intrasexual competition plays an important role in shaping rank-related performance and reproductive skew (Cowlishaw & Dunbar, 1991; Gogarten & Koenig, 2013). They also suggest that a male’s reproductive performance may be better predicted by his proportional social rank, that is, the relative number of males ranked above and below him, and his ability to cope with the costs of intra-sexual competition than by his ordinal rank, that is, the number of males ranked above him.

Intrasexual competition over acquisition and maintenance of social rank and over access to mates can cause costly changes in physiological traits such as the concentration of glucocorticoids (Creel et al., 2013; Goymann & Wingfield, 2004). Glucocorticoids are key physiological mediators of the endocrine control mechanisms that regulate essential biological functions (McEwen & Wingfield, 2003) and covary with individual life history and fitness (Dantzer et al., 2016; Rickefs & Wikelski, 2002). An acute increase in glucocorticoid concentrations usually constitutes an adaptive physiological response to a brief challenge. In contrast, maintaining elevated glucocorticoid concentrations in response to sustained or repeated exposure to challenges can disrupt an individual’s endocrine control mechanism and its ability to respond adequately to subsequent challenges; the individual enters a state in which the physiological mediators themselves may cause pathologies (e.g. delayed wound healing, immunosuppression and disruption of oocyte maturation) and impair fitness (DuRant et al., 2016; MacLeod et al., 2018; McEwen & Wingfield, 2003; Romero et al., 2009; Young et al., 2006). Individuals are therefore constrained in the range of adaptive physiological responses (or ‘reactive scope’; Romero et al., 2009) and are under selection pressure to adopt behavioural responses that minimise their risks of entering such a pathological state. Males occupying a rank at the top and at the bottom of the hierarchy typically differ in their exposure to social conflicts and the availability of coping outlets. By definition, high-ranking males are relatively more likely to win than to lose an agonistic interaction and have more targets they can dominate compared to low-ranking males. High-ranking males may also have more coalition partners and stronger social bonds than low-ranking males (Gilby et al., 2013; Schülke et al., 2010; Vullioud et al., 2019). Dominating a social interaction may elicit a weaker increase in glucocorticoid concentrations and lead to a faster recovery to pre-conflict concentrations than defeat (Koolhaas et al., 2011). Being able to redirect aggression towards a lower-ranking third party or ‘scapegoat’ after being defeated and having strong social bonds or coalitionary support can further serve as coping outlets and social buffer that enable individuals to downregulate glucocorticoid concentrations (Abbott et al., 2003; Sapolsky, 2005; Young et al., 2014). Males that rank proportionally low in the hierarchy may thus have less of a buffer to cope with socially induced elevations in glucocorticoids and thereby experience stronger physiological constraints (DuRant et al., 2016; Romero et al., 2009). In species with long breeding tenures or multiple breeding seasons, low-ranking males may therefore be under stronger selection pressure than high-ranking males to adjust both their social and sexual behaviour in ways that minimise their exposure to intrasexual competition and downregulate their glucocorticoid concentrations (Briffa & Sneddon, 2007; Raulo & Dantzer, 2018; Wingfield & Sapolsky, 2003).

KEYWORDS
allostatic load, coping outlets, dispersal, mate quality, reactive scope, reproductive performance, resource allocation, social status
A number of socio-endocrine studies compared the glucocorticoid concentrations of high-ranking and low-ranking males during and outside the breeding season to assess the physiological costs of investment in sexual activities and intrasexual competition (e.g. Corlatti et al., 2012; Creel, 2001; Gesquiere et al., 2011; Girardi-Buttoz et al., 2014; Setchell et al., 2010). These studies emphasised the physiological costs or ‘allostatic load’ borne by high-ranking, actively competing males and how these costs may constrain their performance and reproductive share within the social group (Port & Kappeler, 2010). Most of these studies were conducted on species where only top-ranking males invest in sexual activities or engage in physiologically and energetically costly sexual behaviours, such as mate-guarding—whereby a male consorts with a receptive female and aggressively disrupts attempts by lower-ranking males to approach or mate with the female—whereas subordinate males forgo reproduction or adopt alternative reproductive tactics (Taborsky et al., 2008) that circumvent direct competition such as opportunistic sneaky copulation. These studies could not disentangle the potential effects of male social rank, investment in sexual activities and male exposure to social conflicts on allostatic load. We therefore currently lack understanding of whether and how rank-related physiological constraints mediate variations in male investment in courtship, reproductive performance, and ultimately, reproductive success among males of different social rank (Bechner & Bergman, 2017; Briffa & Sneddon, 2007: Cavigelli & Caruso, 2015). In addition, the possibility that male investment in sexual activities may not only depend on the physiological costs of sexual activities and mate competition but also be constrained by the time and physiological resources allocated to social activities—i.e. agonistic and affiliative social interactions that enable males to foster social bonds, form coalitions, establish and maintain their social rank, and are essential for male social integration—has not been considered (see also Port & Cant, 2014; Raulo & Dantzler, 2018; Rimbach et al., 2016).

Here, we addressed these gaps and investigated whether the social correlates of male social rank mediate the interplay between glucocorticoid concentrations and male investment in social and sexual activities in the spotted hyena Crocuta crocuta. Spotted hyenas are long-lived social carnivores that live in large clans characterised by a stable linear hierarchy (East & Hofer, 2001), fission–fusion dynamics (Smith et al., 2008), male-biased dispersal (Höner et al., 2007) and promiscuous breeding with no distinct breeding season (East et al., 2003; Engh et al., 2002). Male reproductive success strongly and positively correlates with male social rank (Davidian et al., 2016) but in contrast to many species, this is not the result of female mate preference for particular rank-related male attributes nor of rank-related fighting ability and competitive exclusion. Female spotted hyenas have control over copulation owing to the masculinisation of their outer genitalia (East et al., 1993; Szykman et al., 2007); they are not sexually coerced by males and exercise mate choice. Females prefer males who became members of the clan after they were born (Höner et al., 2007) and males who invest in fostering a relationship with them (East et al., 2003; Szykman et al., 2001). Male spotted hyenas do not adopt alternative reproductive tactics but they do express various behaviours to foster relationships with and express their sexual interest in females (Szykman et al., 2007); these behaviours are here referred to as ‘sexual activities’ or ‘courting’ (see Section 2 for details).

Dominance relationships and social ranks among spotted hyenas are established following social conventions based on asymmetries in the number of coalitionary supporters within a clan rather than intrinsic attributes (Vullioud et al., 2019). These relationships are reinforced through ritualised greetings (i.e. reciprocal ano-genital inspections) and low-intensity agonistic behaviours (Curren et al., 2015; East et al., 1993; Smith et al., 2010). Among males, sexually active native or ‘philopatric’ males occupy a social rank above all immigrant males throughout their tenure (Vullioud et al., 2019). New immigrant males join the new clan at the bottom of the social hierarchy and thereafter follow strict ‘queuing’ conventions: they usually increase in (ordinal) social rank only when a male occupying a rank above them dies or (re)disperses (East & Hofer, 2001). Male–male physical aggression over social rank and access to females is very rare (East & Hofer, 2001). Males are also rather tolerant towards other males when females are present; they rarely exclude or prevent lower-ranking males from approaching a female and mainly compete over the most proximate position to a female (East & Hofer, 2001; Frank, 1986). As a result, multiple males can simultaneously court a given female and remain in her proximity over extended periods of time. Because of the asymmetries in the number of coalition partners between males and the rigidity of the linear social hierarchy, males occupying a rank at the top of the male hierarchy have more opportunities to dominate other males and have more coping outlets than males occupying a rank at the bottom of the male hierarchy (Curren et al., 2015; Smith et al., 2010). These asymmetries are best approximated by male proportional social rank (see Section 2 for details).

We used measurements of faecal glucocorticoid metabolite concentrations (fGMC) as biomarkers of allostatic load (Goymann & Wingfield, 2004) and combined fGMC with the proportional ranks and behavioural data from 319 males of the eight social groups (‘clans’) inhabiting the floor of the Ngorongoro Crater in Tanzania. We tested whether (a) male fGMC vary with social and sexual activities, (b) male proportional rank mediates fGMC in these contexts, and whether males of different rank differ (c) in their investment in social integration and reproduction and (d) in how they allocate their investment among females of different reproductive value.

According to the physiological constraints hypothesis, fGMC should decrease with increasing male proportional rank when males are exposed to intrasexual competition, that is, when they engage in social interactions with other male clan members or when they are sexually active and concurrently interact with male competitors. We further predicted that fGMC should not vary with male proportional rank when males do not interact with other males (e.g. when alone or when courting females in the absence of male competitors), and that fGMC should be lowest when males spend time alone. If so, low-ranking males should experience stronger physiological constraints than high-ranking males. This should be reflected in their activity budget: they should spend relatively more time alone, conversely invest less
in social and sexual activities than high-ranking males, and should focus their investment on females of low reproductive value, who are least competed for (East & Hofer, 2001; Szykman et al., 2007). In contrast, philopatric males should face weaker physiological constraints than immigrant males owing to their high social rank. They should also face weaker social constraints than immigrant males because they have pre-established social bonds with relatives and are better socially integrated owing to their native origin (Vullioud et al., 2019). Philopatric males should therefore invest less in social and more in sexual activities than immigrant males and focus their investment on females of high reproductive value.

2 | MATERIALS AND METHODS

2.1 | Study area and population

All hyenas of the eight resident clans inhabiting the 250-km² floor of the Ngorongoro Crater (3°11′S, 35°34′E) in Tanzania were monitored between April 1996 and November 2015. We conducted behavioural observations and sample collection throughout the day (between 06:00 and 19:00 hr) at resting places, communal and birth dens and other areas of clan territories. Spotted hyenas of this population maintain comparatively high levels of activity during daytime (Kruuk, 1972: the authors, unpublished data); this is probably the consequence of the high altitude (1,800 m) of the Crater floor and associated cool daytime temperatures (monthly average 23.0°C; range = 12.1–31.0°C). The hyenas were individually recognised by their unique spot pattern and ear notches. Their age (±7 days) was estimated based on pelage characteristics, body size, locomotory abilities and behavioural development (Pournelle, 1965). Dispersal is strongly male-biased; approximately 85% of males leave their natal clan and immigrate into another Crater clan to breed whereas virtually all females remain in their natal clan throughout their life (Davidian et al., 2016; Höner et al., 2007). Extra-clan paternity is extremely rare; male breeding prospects therefore depend on their clan membership and the number of young females in the clan (Davidian et al., 2016; Höner et al., 2007, 2010). The number of adult (≥24 months old) clan members and reproducitively active males increased during the study period from 15.5 ± 3.4 to 42.9 ± 5.9 and from 4.0 ± 1.1 to 13.1 ± 2.2, respectively.

2.2 | Male dispersal status

We defined philopatry and dispersal as the outcome of breeding-clan selection that led a male to choose and start his reproductive career in his natal clan or in another clan respectively (Davidian et al., 2016). We considered a male to have chosen a clan when he expressed sexual behaviours toward females and/or invested in joining the social hierarchy of sexually active males in the natal clan (philopatric male) or another clan (immigrant male) for at least 3 months. The date of clan choice was the date of first observation of such behaviour for philopatric males and of first sighting in the new clan territory for dispersers, and defined the start of a male’s tenure. Males who did not show any sign of sexual activity or had not met the 3-month criterion before their date of last sighting or the end of the study period were excluded from the analyses. By applying these criteria instead of an age-based categorisation of males, we avoided potential biases in male behaviour and physiology between philopatric and immigrant males that could arise from differences in sexual motivation and maturity (Akinyi et al., 2017; Davidian et al., 2016; Höner et al., 2008). During the study period, 319 males chose to breed in a clan in the Crater population; 43 Crater-born males started their reproductive career in their natal clan, 253 males dispersed to another Crater clan and 23 males immigrated into Crater clans from elsewhere. We considered both first-time selectors and males who engaged in breeding dispersal, i.e. males who (re)dispersed from their clan of first choice and immigrated into another Crater clan (secondary clan choice). As a consequence, philopatric males can become immigrants and the social rank of immigrant males in our dataset did not strongly correlate with their age.

2.3 | Proportional social rank

Individual social rank was determined on the day of collection of faecal and behavioural data. At the beginning of the long-term research project on spotted hyenas in the Ngorongoro Crater (in April 1996), a sociometric matrix was tabulated for each clan based on the outcome of dyadic agonistic interactions when 80% of all dyads between clan members were observed at least once. The individual with the highest proportion of wins was assigned the ordinal rank 1 and the one with the lowest proportion of wins was assigned the ordinal rank equal to the number of clan members. This matrix was then continuously re-ordered iteratively such that the number of inconsistencies (dyads in which the lower-ranking individual dominates the higher-ranking one) and the difference from the order in the previous period were minimised (Schmid & de Vries, 2013; Strauss & Holekamp, 2019). This ensured that individuals maintained their rank over time unless interaction data suggested otherwise. Before re-ordering, new individuals were added to the order and assigned a rank according to rules and conventions spotted hyenas strictly adhere to when establishing and maintaining dominance relationships (Vullioud et al., 2019). These conventions included (a) offspring acquire the rank just below their mother—a process known as ‘maternal rank inheritance’ (East et al., 2009; Holekamp & Smale, 1991)—and (b) immigrant males join a clan at the bottom of the hierarchy and usually only increase in rank when a higher-ranking clan member dies or disperses—a process known as ‘social queuing’ (East & Hofer, 2001) and that is also observed in female chimpanzees (Foerster et al., 2016), male rhesus macaques (Dubuc et al., 2011), and male Kinda baboons (Petersdorf et al., 2019). The ordinal ranks were then converted into proportional ranks, using the formula: Proportional rank_{i} = ([number of clan members - ordinal rank_{i}]/[number of
clan members – 1/2)) – 1. Male proportional rank was calculated considering as clan members all philopatric and immigrant male members of the focal clan. Female proportional rank was calculated considering as clan members all sub-adult (≥12 months old) and adult clan members of both sexes born in the focal clan. Proportional rank ranges from −1 (lowest rank) to +1 (highest rank). Individuals with a proportional rank within the top, middle and lowest third of the total range were classified as high-ranking, medium-ranking and low-ranking respectively.

Using proportional ranks instead of ordinal ranks has several advantages regarding our study system and questions. In contrast to ordinal ranks which indicate the number of males ranked above a focal male and remain unchanged when new immigrants join the clan at the bottom of the hierarchy, proportional ranks account for all demographic changes within a clan and for differences in the number of clan members between clans (see also Levy et al., 2020). Proportional rank reflects the proportion of clan members ranked above and below a focal individual; proportional rank can thus be used as an integrated measure of the ratio of dominance and coping opportunities (i.e. display dominance, employ scapegoating, enjoy coalitional support and social buffer) to the challenges received by an individual. In spotted hyenas, males are as likely to associate with males that occupy a rank immediately above them as with males ranked immediately below them (Smith et al., 2007); male likelihood to express (or be the target of) agonistic or dominance acts increases with increasing number of lower-ranking (or higher-ranking) males in proximity (Curren et al., 2015). Thus, when males interact with other males, the type and direction of expressed behaviours should generally match those predicted by their proportional rank. Also, note that there is currently no evidence that, in spotted hyenas, rank acquisition and dynamics are caused by fluctuations in the concentration of glucocorticoids or testosterone.

2.4 | Faeces collection, hormone analysis and assessment of allostatic load

We measured fGMC in 361 faecal samples from 120 males, including 52 samples from 13 philopatric and 309 samples from 107 immigrant males (median = 3 samples per male, range = 1 – 17). Faeces were collected immediately after defaecation, mixed, subsampled and stored in liquid nitrogen until transported to Berlin (Germany) on dry ice where they were stored at −80°C until further processing. Faecal subsamples were freeze-dried prior to steroid extraction and fGMC quantified using an in-house competitive enzyme-linked immunosorbent assay (ELISA) based on an antibody generated against cortisol-3-CMO that was previously analytically and physiologically validated for spotted hyenas (Benhaim et al., 2012). Aliquots were extracted and assayed in a single batch; measurements were performed in duplicates and results were accepted only when their coefficient of variation (CV) was ≤5%. Intra-assay and inter-assay CVs were 2% and 15% for the low faecal control pool, and 1% and 8% for the high control pool respectively (for more details on extraction and assay protocol, see Davidian et al., 2015). Measurements are expressed as nanogram per gram (ng/g) of dry faecal matter. Measurements of glucocorticoid metabolites from faeces provide an integrated measure of the endocrine activity over a relatively long period of time (i.e. from hours to days, depending on excretion frequency and food transit; Goymann, 2005). Measurements from faeces reflect the combination of baseline concentrations, endocrine responses to social conflicts (of potentially varying amplitude and frequency), post-conflict recovery (of varying latency) and downregulation by use of coping outlets and social buffer, and therefore are a biomarker for the cumulative physiological costs imposed on the body or ‘allostatic load’ (Goymann, 2005; Goymann & Wingfield, 2004). For the analysis of the social correlates of fGMC, we matched each faecal sample and associated fGMC to the activity (see section below for definitions and methods) the focal male expressed during the period between 36 hr and 10 hr prior to defaecation. This period was defined based on the period during which the physiological response to a challenge induced experimentally is detected in faeces of spotted hyenas (Benhaim et al., 2012). If a male had been monitored for <2 hr (continuous or cumulated) or less than three scans during that period, his activity was considered unknown and the faecal sample was excluded from the model (N = 85 faeces with unknown male activity).

2.5 | Behavioural and proximity data

We collected behavioural and proximity (presence and number of other clan members) data for 319 males using instantaneous scans as well as all-occurrence and focal animal sampling; behaviours were monitored via direct observations and video recordings from a research vehicle. Scans of a given male were conducted a minimum of 60 (±5) min apart, starting at the time of first sighting of the focal male on the same day. Owing to the fluid fission–fusion social dynamics of spotted hyena clans, males and females spend time alone or in subgroups of varying size and composition (with a mean turnover rate of 1 hr), and all clan members are seldom sighted together (Smith et al., 2008); conducting scans on an hourly basis is therefore appropriate to capture these dynamics.

We categorised male activity as ‘social’, ‘sexual’ or ‘alone’ using definitions adjusted to the two main analyses and that were conservative with respect to our predictions. For the analysis of the relationship between male exposure to intrasexual competition on fGMC, males were assigned an activity based on observations of his behaviour during the 10–36-hr period that preceded defaecation. The male was considered socially active whenever he had been involved in affiliative or agonistic interactions with other males—e.g. ritualised greeting, social sniffing, scapegoating, coalition displays (as emitter or target), reconciliatory and appeasement displays and dominance displays in the context of feeding (East et al., 1993; Smith et al., 2010)—and when he had not engaged in any sexual activity during that period. Scapegoating refers to a conspicuous behaviour whereby the target of a dominance act immediately redirects...
dominance (e.g. approaches with its tail up) onto a bystander of lower social rank. Scapegoating is frequent in spotted hyenas and often takes the form of a cascade where successive targets redirect dominance onto a lower-ranking third party (Sapolsky, 2005); when no lower-ranking individual is present, the lowest-ranking individual involved in such cascades may redirect dominance towards a smaller carnivore, bird, rock or even the research vehicle (authors’ personal observation). The male was considered as sexually active whenever he engaged in repeated intersexual investigatory behaviours, repeated short bouts of approach–retreat courtship displays, prolonged following of a female or ‘shadowing’, harassment and mating (Holekamp & Smale, 1998; Szykman et al., 2007). We considered two contexts of sexual activity: (a) sexually active with others, whenever the focal male exhibited sexual behaviours towards a female and concurrently interacted with other males—typically within the context of intrasexual competition—and (b) sexually active alone, when the focal male engaged in sexual activities but did not concurrently interact with another male. We considered the male alone when he had not engaged in any social or sexual activity during that period, i.e. the male had been resting, travelling, hunting or feeding more than 50 m away from other males—a distance at which males are unlikely to be the target of agonistic behaviours, such as scapegoating (East & Hofer, 2001)—or had been observed within 50 m from male clan members but not engaging in any social or sexual activity.

To test whether different types of sexual behaviour were associated with different fGMC—e.g. due to differential levels of male sexual arousal (Koolhaas et al., 2011)—we compared the fGMC of males who displayed the two main types of sexual behaviour, namely, approach–retreat courtship displays and shadowing. We matched fGMC by male identity and social rank and—to avoid potentially confounding effects of intrasexual competition—compared the fGMC of only those males who were sexually active alone, i.e. when intrasexual competition was absent. We found that both types of sexual behaviour were associated with similar fGMC (Wilcoxon signed-rank test; V = 26, p = 0.73, N = 9; median of between-group differences = 0.76 ng/g, CI95% = −7.89 to 22.19 ng/g). We therefore did not distinguish between the types of male sexual behaviour in our analyses.

For the analysis investigating the relationship between rank-related physiological constraints and male activity budget, we used instantaneous scans (N = 21,956 hourly scans, median = 44 scans per male, range = 6–349). The male was considered (a) in social proximity when he engaged in social activities or when he was resting, travelling, hunting or feeding and at least one other clan member of either sex was present within 50 m at the time of the scan, (b) sexually active with others whenever he engaged in sexual activities and at least one other immigrant or philopatric male was present within 50 m, (c) sexually active alone when he engaged in sexual activities and no other immigrant or philopatric male was present within 50 m, and (d) alone when no clan member of either sex was present within 50 m of the focal male at the time of the scan. Note that our assessment of male activity budget, in particular the proportions of scans males were observed alone and in proximity to other clan members, are unlikely to be driven by hunting and feeding patterns or by differential patterns of hunting and feeding across social ranks. Spotted hyenas most often hunt alone and feed in groups; during daytime, hunting and feeding make up <5% of all sightings and males of all social ranks hunt at similar rates (Holekamp et al., 1997; Kruuk, 1972; Smith et al., 2008). Furthermore, differences in fGMC between low-ranking and high-ranking male hyenas are unlikely to arise from rank-related nutritional status. Previous studies indicated that food deprivation can either induce prolonged, elevated glucocorticoid concentrations or an increased amplitude of the stress response in socially challenging contexts, and thereby reveal or amplify differences between high-ranking and low-ranking individuals when nutritional state is correlated with social rank (Killen et al., 2013). In spotted hyenas, low-ranking individuals do have reduced access to food when feeding at kills with higher-ranking clan members. Yet, there is currently no evidence suggesting that low-ranking males suffer from food deprivation since they often hunt and feed on their own and have similar body size and body mass to high-ranking males (East & Hofer, 2001; Engh et al., 2002; Holekamp et al., 1997).

2.6 Statistical analyses

Statistical analyses were conducted using R software v.3.6.3 and associated packages (R Core Team, 2020). Data are presented as means ± SD unless stated otherwise. The threshold for significance was set to 5% for deterministic statistical analyses.

2.6.1 Relationship between male proportional rank, activity and fGMC

We assessed the factors that correlated with fGMC using a general linear mixed-effects model (GLMM; function lmer() in package lme4; Bates et al., 2015). fGMC were normalised using natural-logarithmic transformation prior to analyses. Covariates included male proportional rank, the type of activity (four categories: alone, socially active, sexually active alone and sexually active with others), the interaction between male proportional rank and activity and male origin, i.e. whether the male had grown up in the focal clan (‘native’, for philopatric males) or another clan (‘foreign’, for immigrant males). We additionally controlled for male age (in years; fitted as first- and second-order polynomials) and faeces mass (four categories; ‘small’ [<150 g], ‘medium’ [150–300 g], ‘large’ [>300 g] and ‘unknown’). Faeces mass was considered as a covariate to control for potential ‘dilution effects’ on fGMC (Goymann, 2012). We included male identity as an individual-level random factor. Regression coefficients were estimated by maximum likelihood using Laplace approximation. Significance of fixed effects was assessed as the marginal contribution of each covariate to the full model by subtracting the likelihood of the reduced model without the specific covariate from the full model; p-values were calculated using parametric bootstrapped likelihood ratio tests with
1,000 simulations (package `pbkrtest`; Halekoh & Højsgaard, 2014). Model residuals satisfied the assumptions of normal distribution and homogeneity of variances (residual plots), and did not show signs of multi-collinearity between fixed effects (correlation matrix and squared generalised variance inflation ratios below the widespread critical threshold of 4; Fox & Monette, 1992). We further assessed the significance of the relationship between male social rank and fGMC for each type of activity (slope comparison to zero) and compared the slopes (contrast analysis) when males were alone versus socially active, when sexually active alone versus sexually active with others, and when socially active versus sexually active with others, using the function `emtrend()` in package `emmeans` (Lenth, 2018); p-values for the contrast analysis were adjusted for multiple comparisons using Bonferroni corrections.

### 2.6.2 Relationship between rank-related physiological constraints and male activity budget

We investigated the factors that correlated with male activity budget using a Bayesian multinomial logistic mixed-effects model (multinomial GLMM) based on Hamiltonian Monte Carlo algorithms, using the packages `rstan` (Stan Development Team, 2020) and `rethinking` (McElreath, 2016). Such a multinomial modelling approach is particularly well suited to the structure of observational data—for which the basic unit of analysis is the behaviour that an individual expressed at a given time—and to investigate time-based behavioural trade-offs, such as those arising from activity budgets (Koster & McElreath, 2017); it recognises time as a limited resource and considers that the time an individual allocates to a given activity inherently reduces the time it can allocate to other activities. For model fitting, we specified four chains of 7,000 iterations, half of which were allocated to the warm-up phase. We considered that at each hourly sighting (N = 21,956), a focal male could express one of three categorical behavioural responses: be alone, be in social proximity to other clan members or be sexually active. Fixed effects were male proportional social rank, origin, age and the number of philopatric and immigrant male members of the clan as well as the rank of the courted female; male identity was considered as a random factor. The multinomial model contrasted the odds of expressing a given behaviour relative to the reference behaviour (here, alone). The coefficients estimated by the model were log(odds) and were converted into odd ratios, using the formula: \( \exp[\text{coefficient}] \). Odd ratios > 1 and odd ratios < 1 indicate a relative increase and decrease, respectively, in the likelihood to express the behaviour. We considered a fixed effect significant if the credible interval (CrI\(_{95\%}\)) of its estimated coefficient did not include 1. The model also has the advantage of providing information on the variance of individual-level random effects for each behavioural response as well as their correlation across responses, thereby potentially revealing if individuals who regularly engage in one activity also invest relatively more or less in another activity (Koster & McElreath, 2017). Because the multinomial model examines the proportional allocation of time to social and sexual activities relative to the reference behaviour, the total time considered for each fit corresponds to a subset of all possible behavioural responses and of the activity budget; model estimates thus do not provide information on the effect of the covariates on the overall proportion of total sightings males allocated to each activity (i.e. relative to the combined number of sightings allocated to all other activities). We therefore investigated the extent to which male proportional rank and origin influenced male probability to allocate time to each activity, using the model predicted probabilities and their 95% percentile intervals, as calculated from the posterior samples of the model (for further details on the procedure and R codes, see Koster & McElreath, 2017).

### 2.6.3 Male exposure to intrasexual competition and reproductive value of courted females

Previous studies conducted in other populations showed that female hyenas of high social rank are courted by males at higher rates than low-ranking females (East & Hofer, 2001; Szykman et al., 2007), suggesting that male–male competition for access to females increases with increasing female social rank and associated reproductive value. Siring offspring with a high-ranking female provides substantial short- and long-term fitness benefits to males; their offspring survive better to adulthood, benefit from ‘silver spoon’ effects in terms of increased reproductive success and contribute more to future generations than offspring of lower-ranking females (Davidian et al., 2016; Hofer & East, 2003; Holekamp et al., 1996; Höner et al., 2010). We therefore investigated whether female social rank—here, used as a proxy for female relative reproductive value—and male characteristics correlated with male exposure to intrasexual competition when they courted a female. We used hourly counts of the number of males in proximity to a focal male and his courted female. Because the data were both overdispersed and zero-inflated, we conducted a hurdle model using the function `glmmadmb()` in package `glmmADMB` (Fournier et al., 2012). Such a procedure allows to analyse overdispersed, zero-inflated count data in two steps, each step specifying a distinct underlying process: (a) a binomial process to investigate the factors influencing the presence (sexually active with others coded as ‘1’) versus absence (sexually active alone coded as ‘0’) of males in proximity to a focal male (2,034 sightings of 218 males) and (b) a truncated count process—here, a truncated negative binomial model to circumvent the overdispersion of residuals—restricted to counts with value \( \geq 1 \), to assess the factors that influenced the number of males in proximity when focal males were sighted in the context sexually active with others (1,399 sightings of 197 males). Covariates included male proportional rank, origin and age, the number of philopatric and immigrant male members of the clan as well as the rank of the courted female; male identity was considered as a random factor. Finally, we performed a logistic GLMM to assess the effects of male social rank and origin on male likelihood to court females of high social rank as opposed to females of low and medium social rank.
3 | RESULTS

3.1 | Relationship between male proportional rank, activity and fGMC

There was a significant effect of the interaction between male proportional rank and the type of activity males engaged in on their fGMC (LR = 18.10, p < 0.001; whole model: LR = 125.53, p < 0.0001, N = 361 faeces with matched activity from 120 males; see Table S1 for detailed model estimates). fGMC strongly decreased with increasing proportional rank when males were socially active (social: slope coefficient = −0.56, CI95% = −0.84 to −0.28, p < 0.001; contrast slope alone − social = 0.41, t-ratio = 2.6, p = 0.034; Figure 1) and when males were sexually active and concurrently interacting with other males (sexual with others: slope coefficient = −0.41, CI95% = −0.68 to −0.14, p = 0.003; contrast slope sexual alone − sexual with others = 0.64, t-ratio = 3.15, p = 0.005; contrast slope sexual with others − social = 0.15, t-ratio = 0.92, p = 1). In contrast, male proportional rank did not influence fGMC when males did not interact with clan members (alone: slope coefficient = −0.15, CI95% = −0.41 to 0.10, p = 0.23) and when males were sexually active without interacting with other males (sexual alone: slope coefficient = 0.23, CI95% = −0.12 to 0.59, p = 0.20). Male origin had a significant effect on fGMC (LR = 4.83, p = 0.028), with native males having higher fGMC than foreigners. The predicted and observed fGMC of low-ranking immigrants, high-ranking immigrants and (high-ranking) philopatric males for each type of activity are presented in Table S2.

3.2 | Relationship between rank-related physiological constraints and male activity budget

There was a significant relationship between male proportional rank and male activity budget. As male rank increased, the odds that males allocated time to sexual activities and to being in social proximity to other clan members improved (multinomial GLMM; odds ratiosexual = 1.99, CrL95% = 1.78–2.23; odds ratiosocial = 1.51, CrL95% = 1.42–1.61). The relative increase in investment in sexual activities was higher than the increase in investment in social proximity. Male behaviour also varied with male origin: the odds to be in social proximity were lower for native males than for foreigners (odds ratio = 0.57; CrL95% = 0.45–0.73). Native males were as likely as foreigners to be sexually active relative to being alone (odds ratio = 1.25; CrL95% = 0.83–1.87; see Table S3 for complete model results). Investigation of individual-level random effects further revealed (a) a relatively low variance for social proximity (exp(estimate) = 1.41) in comparison to sexual activities (exp(estimate) = 2.29), and (b) a significant positive correlation between male investment in social and sexual activities (0.27; CrL95% = 0.10–0.47), when controlling for the fixed effects. The heterogeneity of random variance indicates that all males had similar propensities to spend time in social proximity to other clan members but differed greatly in their propensity to allocate time to sexual activities. The positive correlation between investment in social proximity and sexual activities indicates that males with a relatively high propensity to invest in social activities also had a high propensity to invest in sexual activities. Inspection of the probabilities predicted by the model confirmed that male social rank and origin both are strong determinants of the activity budget of males (Figure 2). As males increased in social rank, they spent less time alone, more time with other clan members and more time engaging in sexual activities (Figures 2a and 3a low-ranking vs. high-ranking philopatric males). Males of native origin spent more time alone, less time in social proximity and more time in sexual activities than foreigners (Figures 2b and 3a high-ranking immigrants versus high-ranking philopatric males). Overall, males were most often sighted in social proximity to other clan members (mean percentage out of total hourly sightings: 72% ± 13%, N = 319 males), less often sighted alone (21% ± 13%) and least often sighted engaging in sexual activities (7% ± 9%).

![Figure 1](image_url) The influence of social rank and activity on faecal glucocorticoid metabolite concentration (fGMC) in male spotted hyenas. Purple lines depict the relationship between social rank and fGMC (in natural log units; log [ng/g]). Shaded areas indicate 95% confidence intervals as predicted by a general linear mixed-effects model when other covariates were held constant (age: population mean = 6.69 years, origin: foreigner, faeces mass: medium) and without accounting for individual-level random effects. Grey and yellow dots correspond to raw data for immigrant and philopatric males respectively. Ranks are ordinal ranks scaled to the number of immigrant and philopatric male members of the clan; these proportional ranks range from −1 (lowest rank) to +1 (highest rank). Sample sizes were Nalone = 104 faeces (70 males), Nsocial = 95 faeces (61 males), Nsexual (alone) = 56 faeces (33 males) and Nsexual (with others) = 106 faeces (57 males).
3.3 | Male exposure to intrasexual competition and reproductive value of courted females

When males were sexually active, the likelihood that competitors were present (‘Presence model’) and the number of competitors (‘Count model’) that were present strongly increased with increasing social rank of the courted female (Table 1). Male social rank and origin did not have a significant influence on either the presence or the number of competitors in close proximity (Table 1).

When a male was sexually active, the likelihood of him courting a high-quality, high-ranking female strongly correlated with his proportional rank (logistic GLMM: LR = 7.68, \( p = 0.006 \)) and origin (LR = 8.81, \( p = 0.003 \); whole model: LR = 26.10, \( p < 0.001 \); N = 2034 sightings of 218 males; see Table S4 for detailed coefficients). Low-ranking immigrants invested in females of lower rank (mean female proportional rank = 0.17 ± 0.59, \( N = 76 \); Figure 3b) than did high-ranking immigrants (0.44 ± 0.37, N = 78; Mann–Whitney U test; \( U = 2,228.5, p = 0.008 \)), and high-ranking immigrants invested in females of lower rank than did philopatric males (0.55 ± 0.41, N = 36; \( U = 1,057, p = 0.035 \)).

4 | DISCUSSION

Our findings are consistent with the hypothesis that rank-related physiological constraints are a key proximate mediator of variation in investment in social and sexual activities in male spotted hyenas. Consistent with our predictions, fGMC were similar for males of all social ranks when they were on their own or when they courted a female in the absence of male competitors. Furthermore, when males engaged in intrasexual social interactions and when they courted a female and concurrently interacted with male competitors, low-ranking males experienced higher fGMC than when alone or sexually active alone, and their fGMC were higher than those of high-ranking males. These results indicate that differences in fGMC and allostatic load across male social ranks are contingent on interactions with other males and thus most likely arise from rank-related asymmetries in male exposure to social challenge and availability of coping outlets. The lack of a difference between the slopes when males were socially active and when they courted a female and concurrently interacted with other males further confirms that these patterns emerged irrespective of male investment in sexual activities. Previous studies predicted that rank-related differences in allostatic load should only emerge in systems where dominance relationships are unstable or are established and maintained through intense physical contest (Creel et al., 2013; Goymann et al., 2003; Goymann & Wingfield, 2004). Our results demonstrate that intrasexual interactions can also elicit rank-related differences in allostatic load in systems where dominance relationships are formalised by social conventions and where competition over social dominance and access to mates involves low levels of aggression.

Our findings further indicate that the differences in allostatic load between males of different social rank may be substantial enough to
induce disparities in investment in social integration and sexual activities that have implications for their reproductive success. Low-ranking males spent more time alone than did high-ranking males, at the expense of social and sexual activities. Low-ranking males also courted females of lower reproductive value than did high-ranking males. These tactics may constitute an effective behavioural re-
courted females of lower reproductive value than did high-ranking males, at activities that have implications for their reproductive success. Low-ranking males may prefer investing time in court-
ing lower-quality females rather than high-quality females that are usually courted by higher-ranking males as a tactic to increase their chances to be chosen as sire. Yet, this hypothesis is unlikely to be the main driver of the behaviour of male hyenas. In contrast to the physiological constraints hypothesis, it cannot explain the observed differences in the other aspects of the activity budget, specifically, why low-ranking males invest less than high-ranking males in sexual activities (overall and when competitors are absent), why they invest less in social activities, and why they spend more time away from other clan members.

Three findings of our study are consistent with the idea that the allocation of time by males to different activities is shaped by trade-offs between the benefits of these activities and the physiological and missed-opportunity costs associated with them (Briffa & Sneddon, 2007; Dunbar et al., 2009; Marshall et al., 2012; Ricklefs & Wikelski, 2002). They also indicate that the time and physiological resources that males allocate to social integration plays a crucial role in constraining male investment in sexual activities. First, all males spent most of their time in proximity to other clan members, even low-ranking males for which social interactions elicited comparati-
vely high fGMC. This suggests that prominent investment in social integration is compulsory for all males and may reflect the direct and indirect fitness benefits of social activities. In spotted hyenas, as in other group-living species, maintaining proximity to—and interacting with—members of their clan is essential for social inte-
gration and may strongly influence male reproductive success (East et al., 2003; Gilby et al., 2013; Ryder et al., 2009; Schülke et al., 2010; Wiszniewski et al., 2012). Spending time with clan members may further help males locate females, provide males with opportunities to engage in sexual activities, and thereby increase their chances to be chosen as sires. Second, among immigrant males, an increase in social rank was associated with a decrease in fGMC in (social and sexual) contexts involving intrasexual interactions. In line with the prediction from the physiological constraints hypothesis, high-rank-
ing immigrants also invested more time than low-ranking immigrants in social and sexual activities and focused on females of high repro-
ductive value. These differences possibly arise because high-ranking males bear lowest physiological costs and can re-allocate the spare correlation between fGMC and male social rank; Figure S1, see also Goymann et al., 2003). The comparatively low overall investment in sexual activities by low-ranking males and their investment in fe-
males of lower reproductive value likely affects their chances to be chosen as mates and may explain why in spotted hyenas low-ranking males have lower reproductive success than high-ranking males both in terms of the number and the reproductive value of the offspring they sire (Davidian et al., 2016). Our study may thus explain why re-
productive skew can emerge in group-living species independent of the competitive regime and differences in physical attributes among males. We cannot fully exclude the possibility that the differences in the activity budget between males could in part be explained by an alternative mechanism, namely “self-exclusion”, that is indepen-
dent of differences in physiological constraints between males of different rank. Low-ranking males may prefer investing time in cour-
enting lower-quality females rather than high-quality females that are usually courted by higher-ranking males as a tactic to increase their chances to be chosen as sire. Yet, this hypothesis is unlikely to be the main driver of the behaviour of male hyenas. In contrast to the physiological constraints hypothesis, it cannot explain the observed differences in the other aspects of the activity budget, specifically, why low-ranking males invest less than high-ranking males in sexual activities (overall and when competitors are absent), why they invest less in social activities, and why they spend more time away from other clan members.

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ing immigrants also invested more time than low-ranking immigrants in social and sexual activities and focused on females of high repro-
ductive value. These differences possibly arise because high-ranking males bear lowest physiological costs and can re-allocate the spare
TABLE 1  Factors influencing the presence and number of competitors when male spotted hyenas were sexually active. Shown are the regression coefficients and standard errors (SE) in log units, z values, back-transformed coefficients as exp(coef) and the corresponding likelihood ratio (LR) and p-values for each predictor variable. Regression coefficients were estimated by a hurdle model in two steps: a binomial mixed-effect model (whole Presence model: LR = 69.05, p < 0.001; individual-level random effect variance = 0.14; N = 2034 sightings of 218 males) and a zero-truncated negative binomial mixed-effect model (whole Count model: LR = 60.86, p < 0.001; individual-level random effect variance = 0.11; N = 1,399 sightings of 197 males). For the Presence model, exp(coef) corresponds to odd ratios and indicates the factor of change in the likelihood to be sexually active with competitors relative to that of being sexually active without competitors present, with a one-unit increase in the predictor and when other covariates are held constant. For the Count model, exp(coef) indicates the increase or decrease in the absolute number of competitors present with a one-unit increase in the predictor. N male members corresponds to the number of philopatric and immigrant male clan members

| Fixed effect | Coefficient | SE  | z value | Exp(coef) | LR   | p     |
|--------------|-------------|-----|---------|-----------|------|-------|
| Presence model |             |     |         |           |      |       |
| Intercept    | -0.06       | 0.24| -0.25   |           |      |       |
| Female social rank | 0.55         | 0.09| 6.05    | 1.73      | 36.18| <0.001|
| Male social rank | 0.12         | 0.14| 0.84    | 1.13      | 0.71 | 0.399 |
| N male members | 0.05         | 0.01| 4.75    | 1.05      | 22.52| <0.001|
| Male origin (native) | 0.17         | 0.22| 0.77    | 1.19      | 0.59 | 0.440 |
| Male age    | -0.04       | 0.03| -1.49   | 0.96      | 2.22 | 0.137 |
| Count model |             |     |         |           |      |       |
| Intercept    | 0.42        | 0.11| 3.70    |           |      |       |
| Female social rank | 0.12         | 0.04| 3.10    | 1.13      | 9.88 | 0.002 |
| Male social rank | -0.08        | 0.06| -1.24   | 0.92      | 1.53 | 0.218 |
| N male members | 0.03         | 0.01| 6.17    | 1.03      | 37.76| <0.001|
| Male origin (native) | 0.05         | 0.11| 0.45    | 1.05      | 0.20 | 0.655 |
| Male age    | 0.02        | 0.01| 1.40    | 1.02      | 1.96 | 0.162 |
The influence of social rank on the interplay between physiological costs and behaviour, and its consequences for male performance and reproductive success in the spotted hyena

FIGURE 4

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AUTHORS’ CONTRIBUTIONS
E.D. and O.P.H. conceptualisation; E.D., O.P.H. and H.H. methodology; I.H. software; E.D. formal analysis; E.D., O.P.H., B.W. and M.D. investigation; E.D., O.P.H., I.H. data curation; E.D. and O.P.H. writing of original draft; E.D., O.P.H., B.W., I.H., M.D. and H.H. review and editing of draft.

DATA AVAILABILITY STATEMENT
Data are archived in figshare https://doi.org/10.6084/m9.figshare.13317404.v1 (Davidian et al., 2020).

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REFERENCES
Abbott, D. H., Keverne, E. B., Bercovitch, F. B., Shively, C. A., Mendoza, S. P., Saltzman, W., Snowdon, C. T., Ziegler, T. E., Banjevic, M., Garland, T. J., & S. Sapolsky, R. M. (2003). Are subordinates always stressed? A comparative analysis of rank differences in cortisol levels among primates. *Hormones and Behavior*, 43, 67–82. https://doi.org/10.1016/S0018-506X(02)00037-5
Akindi, M. Y., Gesquiere, L. R., Franz, M., Onyango, P. O., Altmann, J., & Alberts, S. C. (2017). Hormonal correlates of natal dispersal and rank attainment in wild male baboons. *Hormones and Behavior*, 94, 153–161. https://doi.org/10.1016/j.yhbeh.2017.07.005
Alberts, S. C. (2012). Magnitude and sources of variation in male reproductive performance. In J. C. Mitani, P. M. Kappeler, R. A. Palombit, & J. B. Silk (Eds.), *Evolution of primate societies* (pp. 412–431). University of Chicago Press.
Alberts, S. C., Watts, H. E., & Altmann, J. (2003). Queuing and queue-jumping: Long-term patterns of reproductive skew in male savannah baboons, *Papio cynocephalus*. *Animal Behaviour*, 65, 821–840. https://doi.org/10.1016/anbe.2003.2106
Andersson, M. (1994). *Sexual selection*, Princeton University Press. 599 p.
Arman, N. C., Stow, A. J., Cantor, M., Leu, S. T., Klarevas-irby, J. A., Chariton, A. A., & Farine, D. R. (2020). Social barriers in ecological landscapes: The social resistance hypothesis. *Trends in Ecology & Evolution*, 35(2), 137–148. https://doi.org/10.1016/j.tree.2019.10.001
mammal, the Galápagos sea lion (Zalophus wollebaeki). Molecular Ecology, 19, 2574–2586. https://doi.org/10.1111/j.1365-294X.2010.04665.x
Port, M., & Cant, M. A. (2014). Reproductive competition among males in multimale groups of primates: Modeling the costs and effectiveness of conflict. International Journal of Primatology, 35(3–4), 746–763. https://doi.org/10.1007/s10764-013-9744-2
Port, M., & Kappeler, P. M. (2010). The utility of reproductive skew models in the study of male primates, a critical evaluation. Evolutionary Anthropology, 19(2), 46–56. https://doi.org/10.1002/evan.20043
Pournelle, G. H. (1965). Observations on the birth and early development of the spotted hyena. Journal of Mammalogy, 46, 503.

R Core Team. (2020). R: A language and environment for statistical computing. Retrieved from https://www.r-project.org/
Raulo, A., & Dantzer, B. (2018). Associations between glucocorticoids and sociality across a continuum of vertebrate social behavior. Ecology and Evolution, 8(15), 7697–7716. https://doi.org/10.1002/ece3.4059
Ricklefs, R. E., & Wikelski, M. (2002). The physiology/life-history nexus. Trends in Ecology & Evolution, 17(10), 462–468. https://doi.org/10.1016/S0169-5347(02)02578-8
Rimbach, R., Restavino, M., Yuen, C.-H., Pillay, N., & Schradin, C. (2016). Contrasting activity budgets of alternative reproductive tactics in male striped mice. Journal of Zoology, 301(4), 280–289. https://doi.org/10.1111/1091-1241
Romero, L. M., Dickens, M. J., & Cýr, N. E. (2009). The reactive scope model—A new model integrating homeostasis, allostasis, and stress. Hormones and Behavior, 55(3), 375–389. https://doi.org/10.1016/j.yhbeh.2008.12.009
Ryder, T. B., Parker, P. G., Blake, J. G., & Loiselle, B. A. (2009). It takes two to tango: Reproductive skew and social correlates of male mating success in a lek-breeding bird. Proceedings of the Royal Society B: Biological Sciences, 276(1666), 2377–2384. https://doi.org/10.1098/rspb.2009.0208
Sapolsky, R. M. (2005). The influence of social hierarchy on primate health. Science, 308, 648–654. https://doi.org/10.1126/science.1106477
Schmid, V. S., & de Vries, H. (2013). Finding a dominance order most consistent with a linear hierarchy: An improved algorithm for the I&SI method. Animal Behaviour, 83, 1097–1105. https://doi.org/10.1016/j.anbehav.2013.08.019
Schülke, O., Bhagavatula, J., Vigilant, L., & Ostner, J. (2010). Social bonds enhance reproductive success in male macaques. Current Biology, 20, 2207–2210. https://doi.org/10.1016/j.cub.2010.10.058
Setchell, J. M., Smith, T., Wickings, E. J., & Knapp, L. A. (2010). Stress, social behaviour, and secondary sexual traits in a male primate. Hormones and Behavior, 58(5), 720–728. https://doi.org/10.1016/j.yhbeh.2010.07.004
Smith, J. E., Kolowski, J. M., Graham, K. E., Dawes, S. E., & Holekamp, K. E. (2008). Social and ecological determinants of fission-fusion dynamics in the spotted hyena. Animal Behaviour, 76, 619–636. https://doi.org/10.1016/j.anbehav.2008.05.001
Smith, J. E., Memenis, S. K., & Holekamp, K. E. (2007). Rank-related partner choice in the fission–fusion society of the spotted hyena (Crocuta crocuta). Behavioral Ecology and Sociobiology, 61(5), 753–765.
Smith, J. E., Van Horn, R. C., Powning, K. S., Cole, A. R., Graham, K. E., Memenis, S. K., & Holekamp, K. E. (2010). Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. Behavioral Ecology, 21, 284–303. https://doi.org/10.1093/beheco/arp181
Stan Development Team. (2020). RStan: The R interface to Stan. R package version 2.19.2. Retrieved from http://mc-stan.org/
Strauss, E. D., & Holekamp, K. E. (2019). Inferring longitudinal hierarchies: Framework and methods for studying the dynamics of dominance. Journal of Animal Ecology, 88(4), 521–536. https://doi.org/10.1111/1365-2656.12951
Surbeck, M., Deschner, T., Weltring, A., & Hohmann, G. (2012). Social correlates of variation in urinary cortisols in wild male bonobos (Pan paniscus). Hormones and Behavior, 62(1), 27–35. https://doi.org/10.1016/j.yhbeh.2012.04.013
Szykman, M., Engh, A. L., Van Horn, R. C., Funk, S. M., Scribner, K. T., & Holekamp, K. E. (2001). Association patterns among male and female spotted hyenas (Crocuta crocuta) reflect male mate choice. Behavioral Ecology and Sociobiology, 50, 231–238. https://doi.org/10.1007/s002650100356
Szykman, M., Van Horn, R. C., Engh, A. L., Boydston, E. E., & Holekamp, K. E. (2007). Courtship and mating in free-living spotted hyenas. Behaviour, 144, 815–846. https://doi.org/10.1163/15685390778147618
Taborsky, M., Oliveira, R. F., & Brockmann, H. J. (2008). The evolution of alternative reproductive tactics: Concepts and questions. In R. F. Oliveira, M. Taborsky, & H. J. Brockmann (Eds.), Alternative reproductive tactics. Cambridge University Press.
van der Jeugd, H. P. (2001). Large barnacle goose males can overcome the social costs of natal dispersal. Behavioral Ecology, 12(3), 275–282. https://doi.org/10.1093/beheco/12.3.275
van Noordwijk, M. A., & van Schaik, C. P. (2004). Sexual selection and the careers of primate males: Paternity concentration, dominance acquisition tactics and transfer decisions. In P. M. Kappeler & C. P. van Schaik (Eds.), Sexual selection in primates: New and comparative perspectives (pp. 208–229). Cambridge University Press.
Vullioud, C., Davidian, E., Wachter, B., Rousset, F., Courtiol, A., & Höner, O. P. (2019). Social support drives female dominance in the spotted hyena. Nature Ecology & Evolution, 3, 71–76. https://doi.org/10.1038/s41559-018-0718-9
Wingfield, J. C., & Sapolsky, R. M. (2003). Reproduction and resistance to stress: When and how. Journal of Neuroendocrinology, 15(8), 711–724. https://doi.org/10.1046/j.1365-2826.2003.01033.x
Wiszniewski, J., Corrigan, S., Beheregayar, L. B., & Möller, L. M. (2012). Male reproductive success increases with alliance size in Indo-Pacific bottlenose dolphins (Tursiops aduncus). Journal of Animal Ecology, 81(2), 423–431. https://doi.org/10.1111/j.1365-2656.2011.01910.x
Young, A. J., Carlson, A. A., Monfort, S. L., Russell, A. F., Bennett, N. C., & Clutton-Brock, T. H. (2006). Stress and the suppression of subordinate reproduction in cooperatively breeding meerkats. Proceedings of the National Academy of Sciences of the United States of America, 103(32), 12005–12010. https://doi.org/10.1073/pnas.0510038103
Young, C., Majolo, B., Heistermann, M., Schülke, O., & Ostner, J. (2014). Responses to social and environmental stress are attenuated by strong male bonds in wild macaques. Proceedings of the National Academy of Sciences of the United States of America, 111(51), 18195–18200. https://doi.org/10.1073/pnas.1411450111
Young, C., McFarland, R., Barrett, L., & Henzi, S. P. (2017). Formidable females and the power trajectories of socially integrated male vervet monkeys. Animal Behaviour, 125, 61–67. https://doi.org/10.1016/j.anbehav.2017.01.006

SUPPORTING INFORMATION
Additional supporting information may be found online in the Supporting Information section.

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