The legacy of privilege: Social inheritance reverses sex differences in reproductive inequality in spotted hyenas

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Abstract

Inequalities in reproductive success among females and males shape natural and sexual selection, as well as genetic diversity. A key mechanism influencing reproductive inequality in humans and other animals is the social inheritance of privilege. Using a 29-year dataset spanning eight generations of spotted hyenas (*Crocuta crocuta*), a species in which social status is maternally inherited, we show that inheritance of privilege associated with high status not only shapes reproductive inequality but can reverse its typical sex bias. As in most polygynous species, reproductive inequality was lower among females than males when estimated on an annual basis. When measured across multiple generations, inequality increased in both sexes but disproportionately so among females. This effect was strong enough to reverse the sex bias in favor of females after a single generation. After only a few generations, most individuals thus descended from female ancestors that held the top-ranking position in their clan. Our study demonstrates the strong impact of the social inheritance of privilege on reproductive inequality by shaping differences between the sexes. We outline how reproductive inequality influences female-female and male-male competition and genetic evolution.

Keywords

Reproductive skew; Intergenerational inequality; Sexual selection; Sex roles; Intrasexual competition; Expected genetic contribution; Non genetic inheritance; Darwin-Bateman paradigm; Multinomial M-index.

Introduction

Reproductive success is often unevenly distributed within animal societies: some individuals contribute many offspring to the next generation while others leave none. When inequality is high, only a few individuals pass on their genes, thereby amplifying genetic drift, mitigating the effect of natural selection, and reducing genetic diversity[1,2]. The extent of reproductive inequality can also reflect the strength of selection on phenotypic traits[3]. Since reproductive inequality often differs between the sexes[4,5], it can also reveal which sex has a greater opportunity for selection and provide information on the intensity of intrasexual competition[6–8].

The Darwin–Bateman paradigm predicts that anisogamy results in stronger sexual selection on males and greater reproductive inequality in males than in females[7,9,10]. Empirical studies that calculated reproductive success over a short period of time, such as a breeding season or a year, confirmed this prediction: in most species, males exhibit higher variance in reproductive success[5,8]. These findings reinforced the view that intrasexual competition is predominantly a male phenomenon, expressed through male–male competition for access to seemingly passive females[11].

However, such short-term measures of reproductive success also reflect biological constraints, especially in females whose limited reproductive output per breeding event restricts the extent of inequality. When reproductive success is assessed across lifetimes, reproductive inequality in females can increase and sex differences in reproductive inequality be reduced and even disappear[12]. Indeed, a growing body of work has emphasized that competition among females is widespread and can exert strong selection[13–16].

Reproductive inequality often results from unequal access to resources such as food and mates[17]. In many animal societies, access to resources is determined by traits that are genetically inherited, such as body size, strength, or weaponry[18–20]. But access to resources can also be determined by traits and resources that are inherited socially, such as the network of allies and social status ("relational wealth"[21–25]) or materials ("material wealth"[26–28]). Social inheritance can thus lead to privilege—the differential access to inherited resources[29]. Privilege can persist across generations and is widespread in human and non-human societies, making it a powerful—but often overlooked— driver of reproductive inequality[17,29,30]. In some societies, privilege is transmitted through maternal lines and in others through paternal lines[21,31–34]. Such sex-specific social inheritance can modify the reproductive inequality of males and females over generations. A multi-generational approach is thus needed to capture and study long-term patterns of inequality[17].

To investigate how social inheritance of privilege shapes reproductive inequality, we analyzed pedigree information from 2,743 individually-known spotted hyenas (*Crocuta crocuta*), spanning 29 years and eight generations, from a free-ranging population inside Ngorongoro Crater, Tanzania. This species is well suited for studying social inheritance because individuals live in clans organized by linear dominance hierarchies, where offspring socially inherit their rank from their mother and a high rank confers privilege[35,36]. High-ranking individuals have priority access to resources and greater social support than low-ranking individuals[35,37,38]. High-ranking females enjoy this privilege throughout their lives, resulting in earlier reproduction, shorter interbirth intervals, higher cub survival and longer lifespan compared to lower-ranking females[39,40]. Sons of high-ranking females also enjoy fitness benefits[41] but these are more limited because, unlike daughters, sons typically disperse to another clan at sexual maturity[42] (but see[43]). Thus, in contrast to females, males typically do not retain the privilege of their natal rank and they do not transmit their rank or privilege to their offspring.

We hypothesized that reproductive inequality across generations is shaped by the social inheritance of privilege. We expected reproductive inequality to be greater in males than in females when estimated by the number of offspring produced due to greater reproductive constraints imposed by the life history of female mammals[12]. We further predicted that inequality would rise faster among females and eventually surpass that among males when including more generations, due to the maternal inheritance of privilege.

Results

Reproductive success in female and male spotted hyenas

We calculated four measures of reproductive success for 287 females and 205 males that reached sexual maturity and had lifetime data available: the (1) annual number of offspring, (2) lifetime number of offspring, as well as the number of (3) grandoffspring and (4) great-grandoffspring. The mean annual number of offspring was lower in females (0.46 ± 0.33; range = 0–1.82; n = 268) than in males (0.74 ± 0.61; range = 0–2.83; n = 188; Wilcoxon rank-sum test: $W = 18{,}695$, $p < 0.001$), based on the analysis of individuals with a minimum reproductive tenure of one year. During their lifetime, females produced fewer offspring (3.80 ± 3.71; range = 0–19; n = 287) than males (4.95 ± 4.73; range = 0–26; n = 205; $W = 25{,}817$, $p = 0.0196$) (Fig. S1). A total of 22.3% of females (n = 64) and 18.5% of males (n = 38) did not produce offspring during their lifetime. On average, female reproductive tenure exceeded male reproductive tenure by 3.8 months (see Supplementary Information Section 2). The mean number of grandoffspring was lower for females (8.23 ± 15.63; range = 0–106; Fig. S2a) than for males (11.29 ± 15.77; range = 0–85; Fig. S2b; W

= 24,236, $p < 0.001$). A total of 47% of females ($n = 135$) and 33.7% of males ($n = 69$) had no grandoffspring. The mean number of great-grandoffspring was also lower for females (7.55 ± 21.18; range = 0–152; Fig. S3a) than for males (10.59 ± 22.88; range = 0–155; Fig. S3b; W = 25908, $p = 0.00835$). A total of 69% of females ($n = 198$) and 58% of males ($n = 119$) had no great-grandoffspring.

Reproductive inequality increases more in females across generations

To quantify reproductive inequality in our four measures of reproductive success, we used the multinomial index (M-index)[44]. This index compares observed reproductive success to that expected under an equal reproductive rate. Reproductive inequality in the annual number of offspring (M_{OYear}) was 0.18 (95% CI: 0.06–0.32) for females and 0.40 (95% CI: 0.25–0.57) for males (Fig. 1a), indicating greater reproductive inequality in males than in females. Reproductive inequality in the number of offspring produced per lifetime (M_{OLife}) was similar in females (0.76; 95% CI: 0.59–0.94) and males (0.78; 95% CI: 0.60–0.99). Reproductive inequality in the grandoffspring number (M_G) was 3.53 (95% CI: 3.12–3.97) in females and 1.91 (95% CI: 1.69–2.15) in males, and reproductive inequality in the great-grandoffspring number (M_{GG}) was 7.50 (95% CI: 6.80–8.29) in females and 4.41 (95% CI: 3.97–4.90) in males.

To complement the M-index and provide a traditional representation of inequality, we computed Lorenz curves[45] (Fig. 1b). At the level of lifetime counts of offspring, the top 19.49% of females and 19.8% of males accounted for 50% of all offspring, indicating similar inequality. However, for grandoffspring, the top 8.22% of females and 12.4% of males produced half of all descendants and, for great-grandoffspring, these values declined further to 3.96% of females and 6.26% of males. Gini coefficients corresponding to each Lorenz curve are provided in Supplementary Table 1.

Thus, reproductive inequality increased across generations in both sexes, but the increase was more pronounced in females than in males, reversing the sex bias in inequality from male to female (Fig. 1).

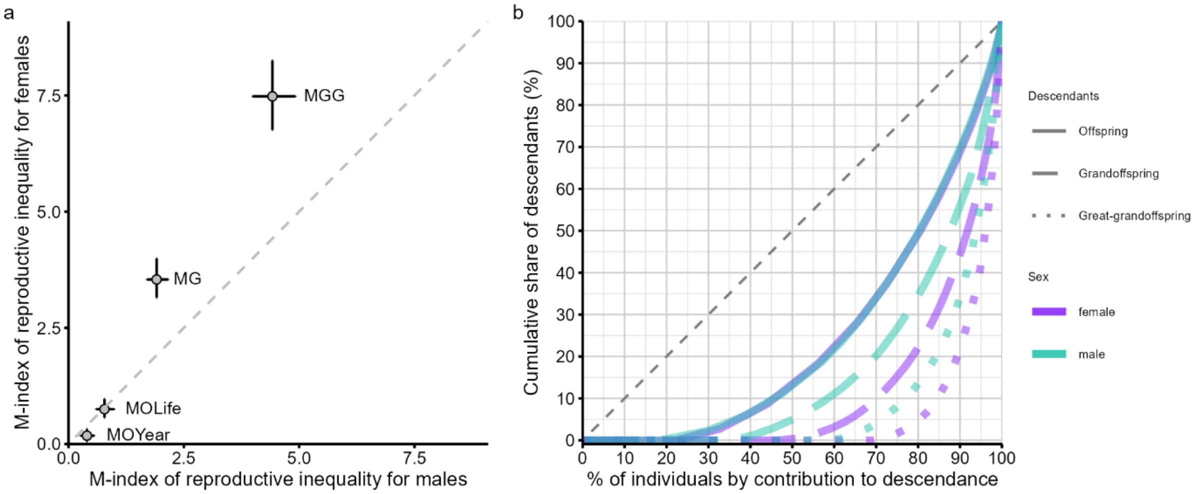

Fig. 1 | Comparison of reproductive inequality in female and male spotted hyenas (a) Relationship between male (x-axis) and female (y-axis) M-indices of reproductive inequality for four measures of reproductive success: annual number of offspring (M_{OYear}), lifetime number of offspring (M_{OLife}), grandoffspring (M_{G}), and great-grandoffspring (M_{GG}). Filled circles are point estimates; horizontal and vertical lines around the circles indicate 95% credible intervals. The dashed diagonal line represents equal M-indices in the two sexes. (b) Lorenz curves depicting the cumulative distribution of descendant production for females and males, across three generations: (lifetime) offspring, grandoffspring, and great-grandoffspring. For each sex, individuals were ordered by their contribution to descendant production, and cumulative percentages were computed to visualize reproductive inequality. Note that male and female curves overlap at the offspring generation.

Stronger intergenerational transmission of reproductive success in females

To clarify why reproductive inequality increases more strongly in females compared to males, we examined the relationship between the number of offspring and the number of grandoffspring across sexes. We found that the (log) number of grandoffspring increased more strongly with the (log) number of offspring in females than in males (zero-inflated negative binomial model; $\chi^2 = 8.32$, df = 1, $p = 0.00332$; Fig. 2; Supplementary Table S2).

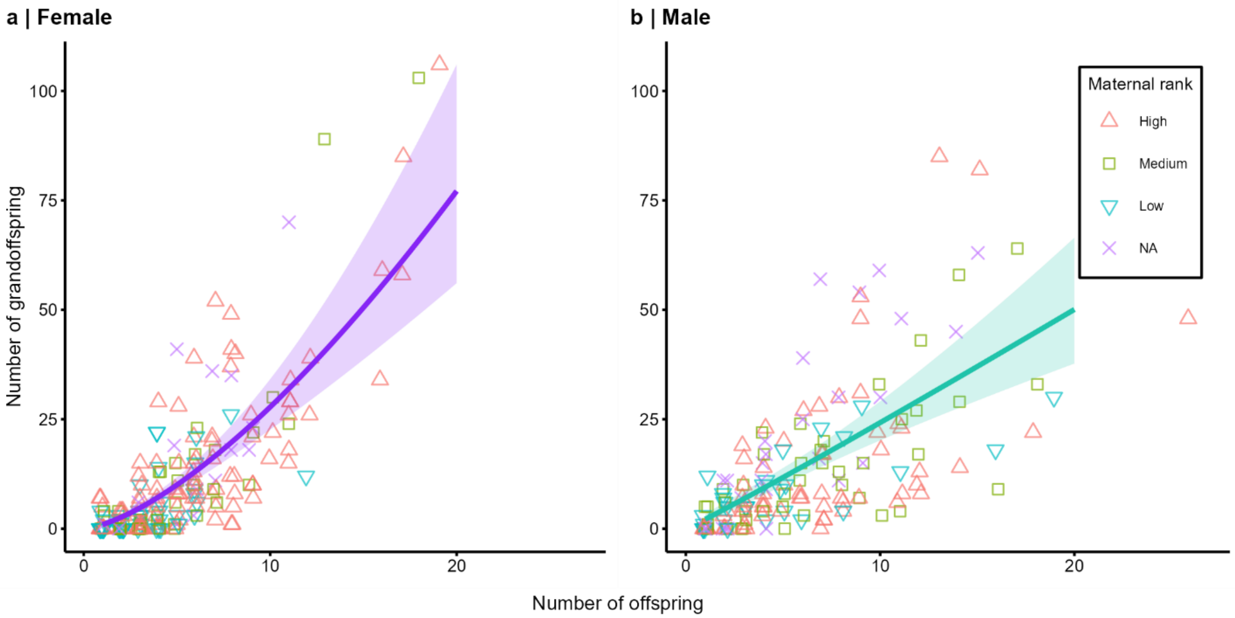

Fig. 2 | Relationship between the number of offspring and the number of grandoffspring produced by female and male spotted hyenas. Panels show the number of grandoffspring as a function of the number of offspring in (a) females (n = 223) and (b) males (n = 167); only individuals who produced at least one offspring are included. Symbols represent individuals, colored and shaped by maternal standardized social rank (High, Medium, Low), and are slightly jittered horizontally for visibility. Solid lines show model-predicted mean numbers of grandoffspring from zero-inflated negative binomial models, with shaded ribbons indicating 95% confidence intervals. Predictions are displayed on the count scale.

Among individuals producing a large number of offspring, the correlation between the numbers of offspring and grandoffspring was particularly strong in females (e.g. for individuals producing 10 or more offspring: Spearman's $\rho_{female} = 0.679$, $n_{female} = 21$ vs. $\rho_{male} = 0.313$, $n_{male} = 34$ in males; $p = 0.0445$). This result reflects the higher proportion of individuals born to mothers of high social rank (for individuals producing 10 or more offspring: 71.4% of females vs. 41.2% of males; see Fig. 2).

Numbers of descendants of high-ranking mothers increase more along maternal than paternal lineages across generations

To explore the long-term, population-level effects of sex-biased rank inheritance, we quantified the distribution of ordinal ranks across maternal and paternal ancestors (Fig. 3). We calculated the maternal rank of all individuals with known ancestry (n = 2,743) or ‘generation zero’ (G0). We then reconstructed genealogical lineages backward in time, identifying the maternal rank of their mother (G1), their maternal grandmother (G2), and so on. For females, this approach captured the direct matriline; for males, we traced the maternal rank of each paternal ancestor (i.e., the father, the father of the father...).

Among females, the proportion of individuals born to top-ranking ‘alpha’ mothers (see darkest red in Fig. 3a) increased markedly across generations traced backwards from G0. In G0, only 9.48% of individuals were born to alpha mothers, compared to 21.6% in G1, 25.7% in G2, 34.2% in G3 and 28.5% in G4. Across these five generations, the proportion of alpha-born females increased 1.32-fold per generation on average. Among males, the proportion of individuals born to alpha mothers showed only a modest, non-monotonic change from G0 to G3 (Fig. 3c). Although the proportion increased from 9.48% in G0 to 16.4% in G1, it declined in subsequent generations to 13.8% in G2 and 11.9% in G3, yielding overall a net change of 1.07-fold. Generations G5 & G6 for females, and G4 for males, were excluded from the fold-change analysis due to the small sample size (n < 20 individuals).

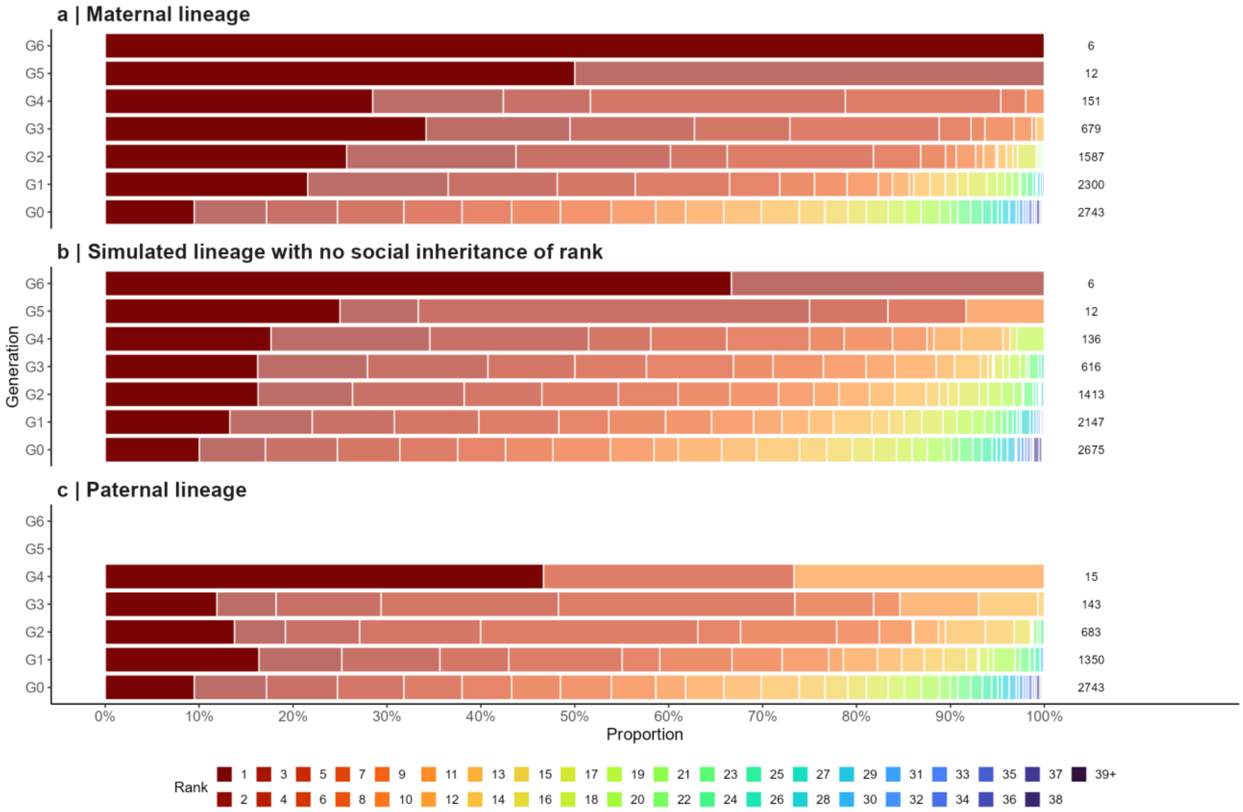

Fig. 3 | Effect of social rank inheritance: distribution of social ranks among ancestors in maternal and paternal lineages. Stacked bars represent the distribution of ordinal ranks of ancestors within a given generation; ranks 39 and lower were pooled. Generation 0 (G0) contains all individuals with known ancestry — before tracing either maternal or paternal ancestral lines. For the maternal lineage (a), the plot shows the maternal ranks of the mothers (G1), maternal grandmothers (G2), and so on of the individuals of G0. In (b) data were generated by permutation of ancestor identities from (a) under a scenario with rank-related reproduction but no social inheritance of rank. For the paternal lineage (c), the plot tracks the maternal ranks of the fathers (G1), paternal grandfathers (G2), and so on of the individuals of G0. Red colors indicate higher ranks and blue colors indicate lower ranks. Numbers on the right of the bars are the numbers of individuals.

Social inheritance increases the prevalence of top-ranking females among individuals' ancestors

Social rank inheritance could increase the proportion of direct descendants of alpha females over generations. To test this, we conducted a permutation analysis that disrupted lineage continuity while preserving rank-related production of descendants. For each focal individual, we reassigned maternal identity by randomly selecting a mother from the same clan who had produced an offspring in the two years preceding the focal individual's birth. This procedure removed social rank inheritance but retained the empirical variation in maternal reproductive success as high-ranking females produce more offspring and are more likely to be assigned as mothers. Across 1,000 permuted datasets, the mean geometric fold-change in alpha rank frequency was 1.15 (see example in Fig. 3b), while the observed value in the maternal lineage was 1.32. No simulated values were equal to, or greater than, the observed values, yielding a permutation p-value < 0.001 (see Fig. S4). Thus, the increase in the proportion of alpha-born ancestors when going backward in time was significantly greater than expected under the null model assuming no rank inheritance. These results demonstrate that social inheritance leads to descendants of alpha females becoming increasingly overrepresented across generations.

Highest share of descendants for alpha females

To evaluate how privilege translates into long-term reproductive success, we determined the social rank of the most successful females, defined as the females with the largest number of living descendants as of January 1st 2023, across the history of each clan (Table 1). Within each clan, most native individuals (between 58% and 100% of clan members) were descendants of the most successful females, all of which had held the alpha position during some period of their reproductive tenure. Those females were also ancestors of many descendants beyond their natal clan.

Table 1 | Alpha status and number of direct descendants of the most successful female spotted hyenas in the eight Ngorongoro Crater clans. All descendant counts and clan characteristics were calculated as of January 1st 2023.

Females			**Descendants**				**Clan**		
			In population		**In natal clan**				
Name	**Alpha**[1]	**Death Year**	**Total**	**Alive**	**Alive**	**%**[2]	**Name**	**Natives**	**Total**
A-013	Yes	2011	566	177	61	68.5	Airstrip	89	102
E-004	Yes	2002	715	164	32	82.1	Engitati	39	50
F-001	Yes	2002	590	174	31	93.9	Forest	33	40
L-007	Yes	1996	1,267	283	37	97.4	Lemala	38	51
M-003	Yes	1996	1,052	243	52	100.0	Munge	52	61
N-005	Yes	2002	577	140	20	62.5	Ngoitokitok	32	35
S-105	Yes	2013	219	51	43	79.6	Shamba	54	63
T-014	Yes	2016	89	31	15	57.7	Triangle	26	33

[1] Alpha indicates whether a female ever held the alpha position in the clan. [2] The percentage reflects the proportion of a female's descendants born in and still alive in her natal clan at the end of the study period, relative to the total number of native individuals alive in that clan.

Grandoffspring number better predicts long-term genetic contribution than offspring number

Given that social inheritance amplifies reproductive inequality over generations, we next asked whether the number of grandoffspring is a better predictor of long-term genetic contribution than the number of offspring. For this, we used the population pedigree to quantify the expected number of copies of a new genetic variant (g_i) that an individual i would contribute to the population at the end of the study period (January 1st 2023). Repeating this computation for 406 individuals (see Supplementary Table S3) revealed that g_i was more strongly correlated with the number of grandoffspring than with the number of offspring (females: Spearman's $\rho_{\text{grandoffspring}} = 0.856$ vs. $\rho_{\text{offspring}} = 0.666$; males: $\rho_{\text{grandoffspring}} = 0.832$ vs. $\rho_{\text{offspring}} = 0.665$; overall: $\rho = 0.856$ vs. 0.646).

DISCUSSION

Reproductive inequality can arise not only from variation in genetically heritable traits that influence reproductive success, but also from non-genetic mechanisms such as the social inheritance of privilege. While the contribution of genetic inheritance to reproductive inequality has been investigated in some detail[46–48], much less is known about the effect of social inheritance of privilege, especially in non-human animals. Here we show that social inheritance of privilege can be a strong driver of reproductive inequality and that it can reverse typical sex differences in reproductive inequality when inheritance is biased towards one sex.

In our study population of spotted hyenas, reproductive inequality in terms of number of offspring produced per year was greater in males than females. This is consistent with previous findings in another hyena population[49] as well as with the general pattern in polygynous human populations and non-human mammals[5]. This difference disappeared when reproductive inequality is measured in terms of lifetime reproductive success, likely reflecting both female short-term reproductive constraints (small litter size, and long gestation and lactation periods) and sex differences in social rank acquisition (females maintain their maternally-inherited rank, whereas dispersing males lose it).

Over longer timescales, reproductive inequality increased in both sexes, but more markedly in females than in males, as predicted for a system where privilege is socially inherited through the maternal line[50]. Females with high reproductive success also produced reproductively successful offspring, as indicated by the stronger offspring-grandoffspring relationship observed in females than in males. Our simulations demonstrate that the social inheritance of privilege, rather than rank-related reproductive output alone, led to an over-representation of top-ranking ‘alpha’ female descendants in the population. Reproductive inequality thus seems to result from privilege. Since high-ranking females recruit more female offspring into their own clan, and since those offspring provide kin support that consolidates high status[51], privilege also results from reproductive inequality. Both privilege and reproductive inequality are thus part of the same positive feedback loop[29].

In our study, sex-biased social inheritance leads to a striking sex reversal in reproductive inequality: while males showed greater inequality in short-term reproductive success, inequality became greater in females as soon as grandoffspring were considered. Classical sexual selection theory predicts that the sex with lower parental investment, usually males, competes for access to the ‘limiting sex’, usually females, and therefore experience a higher reproductive inequality. In species where females invest more in their offspring than males, females can nevertheless show greater reproductive inequality than males when one or a few females monopolize a large share of the reproduction such as in cooperative breeders like the superb starling (*Lamprotornis superbus*), or the meerkat (*Suricata suricatta*)[52–54]. Our results extend this observation by showing that even when no particular female monopolizes reproduction, social inheritance can lead to a similar sex reversal in reproductive inequality provided that reproduction is measured in terms of descendants in future generations.

Such a sex reversal in reproductive inequality is likely to impact both female-female and male-male competition. The concentration of the reproductive value in a few females intensifies female-female competition[55]. In cooperative breeders, females compete for breeding opportunities[53,56], but what do females compete for in systems shaped by social inheritance of privilege? Our findings show that sex-biased reproductive inequality results from a stronger relationship between offspring and grandoffspring numbers in females. This could indicate competition over traits that secure and maintain high rank, and associated privilege that increase the reproductive success of offspring, rather than competition over access to male mating partners. In line with that, female hyenas fight directly over rank, social reversals or ‘coups’ are common[57], and female infanticide—a hallmark of female-female competition across species[58]—is a leading cause of juvenile mortality[59] as well as a behavior that reduces the social support of females whose offspring are killed[51].

Our findings further suggest that social inheritance of privilege reshapes optimal strategies in the ‘competing sex’ and thereby shapes male-male competition: males could achieve higher long-term fitness by targeting high-ranking females, rather than by maximizing their number of matings or mating partners. Consistent with this, high-ranking male spotted hyenas allocate more courtship effort toward high-ranking females and achieve greater reproductive success with them than low-ranking males do[43,60].

Changes in reproductive inequality triggered by the social inheritance of privilege inevitably cascade into genetic consequences at the population level. One immediate consequence is that high-ranking females contribute ultimately much more to the gene pool than low-ranking ones. By hitchhiking on the positive, multigenerational, cascading effect of privilege, the alleles of males mating with privileged females can also reach high frequencies over a few generations. More generally, by increasing the variance in reproductive success, the social inheritance of privilege can have far-reaching repercussions on genetic structure (for a review, see[61]). In our study population, many individuals—particularly females—had no descendants, while a few highly successful females contributed disproportionately to the gene pool (although the genetic contribution of any ancestor inevitably gets diluted over generations[62]). Similar patterns of extreme lineages loss driven by high reproductive variance and heritable differences in fitness were documented in other vertebrates such as cheetahs (*Acinonyx jubatus*)[63]. When reproduction is concentrated in a small subset of individuals, effective population size declines and this can decrease the efficiency of natural selection[2,64,65], accelerate the loss of genetic diversity[1], and elevate inbreeding[64].

Certain behaviors may however buffer populations against the genetic risks brought by the social inheritance of privilege. In spotted hyenas, male-biased dispersal[42,66], female mate preferences[42] and female promiscuity[67] are likely to increase gene flow and reduce inbreeding. Whether such behaviors are sufficient to counter the negative long-term genetic effects, and whether they are more likely to be present in societies with strong social inheritance of privilege remain open questions.

Given the potential impact of the social inheritance of privilege upon genetic evolution, one may wonder, how common is socially inherited privilege a key driver of reproductive inequality? The situation requires privilege to be present, retained within the lineage over multiple generations, and to influence reproductive success. Evidence from both human and animal societies suggest that this situation is not unique to spotted hyenas. For example, among the Gabbra pastoralists, livestock is inherited patrilineally and unequally among sons, and it is a key determinant of marriage opportunities and reproductive success[68]. In American red squirrels (*Tamiasciurus hudsonicus*), mothers may bequeath their food cache to a single offspring, with consequences for its survival and future reproduction[26]. We expect more examples in system where social conventions make the effect of privilege and its inheritance consistent over multiple generations.

Importantly, future studies must consider the social inheritance of privilege in its own right. Indeed, while the social inheritance of privilege shares key features with genetic inheritance (both can show substantial heritability, influence fitness variation, be sex-biased, and exert large consequences on the gene pool), important differences remain. For example, unlike genetic transmission—where all offspring have equal probability of inheriting alleles that enhance the access to resources—social privilege is typically restricted to particular offspring (e.g., the eldest son in many human societies[69]; youngest in spotted hyenas and cercopithecines[21,33,36]). The social inheritance of privilege also recalls cultural inheritance since the transmission of the privilege across generations is not genetic[21]. Yet, contrary to cultural traits, privilege is based on social conventions that seem to vary little across time and space: all spotted hyena clans show linear dominance hierarchies and probably the same mechanisms of rank inheritance.

In conclusion, our study provides strong evidence that the social inheritance of privilege can shape reproductive inequality and contributes to the growing recognition that social inheritance has far-reaching genetic and evolutionary consequences[50,70]. Together, these findings highlight the need to incorporate more complex social dynamics into both theoretical and empirical studies in evolutionary biology and behavioral ecology. In particular, that both female-biased social inheritance of privilege and cooperative breeding are strongly tied to female-female competition calls for research reevaluating the role of females in animal societies.

Methods

Study species and population

Spotted hyenas live in social groups called clans, which have linear dominance hierarchies and a high level of female dominance[51]. Offspring of both sexes acquire a rank just below their mother through behavioral mechanisms of social learning and maternal social support[21,32]. Accordingly, offspring resemble mothers in social ties, especially in high-ranking lineages[23]. Female hyenas typically produce one or two cubs per litter (rarely three), with a lactation period of 12–20 months and an interbirth interval ranging from 6.6 to 28.7 months, limiting their overall reproductive output[37,40,71,72]. Reproduction does not follow a marked seasonal pattern, so generations overlap[37]. Dispersal is strongly male-biased with approximately 85% of males leaving their natal clan before reproducing, and immigrating to a new clan to breed, whereas females are highly philopatric[41–43]. In their new clan, immigrant males lack social support and enter at the bottom of the hierarchy. They progressively increase in rank over time and while they may eventually reach a high rank among immigrants, they will remain lower ranking than native individuals[51,73,74]. High-born males do retain their maternal rank and benefit from priority access to resources during excursions to the territory of their natal clan, but these extended benefits only last up to 2 years after dispersal[41].

We studied the spotted hyenas of the eight resident clans of the 300-km² Ngorongoro Crater in Tanzania (3°11′S, 35°34′E) between April 12th 1996 and February 21st 2025. All individuals were individually identified by their unique spot pattern and other individual morphological features (e.g. ear notches). Most males born in one of the Crater clans choose to breed in a Crater clan[43], which gave us the opportunity to record the reproductive output of philopatric and dispersing males and allowed us to compare females and males. We classified individuals as adults using sex-specific reproductive criteria. Females were adults from 2 years of age onwards as high-ranking females typically start reproducing at that age[35]. In the rare cases when a female conceived before the age of 2 years, she was considered as an adult from the date of conception. Dispersing males were considered adults from their first confirmed sighting in a new clan's territory followed by sustained presence and social integration (marking the start of their tenure). For philopatric males, we considered them as adults from the date they first displayed sexual interest in females and continued doing so for at least three consecutive months[43]. This reflects the longer time males require entering the breeding pool. The average age at adulthood was 2.0 ± 0.02 years in females and 3.38 ± 0.76 years in males. The delayed expression of sexual behaviors in males is also reflected in reproductive data: the median age at first conception (estimated as offspring birthdate minus 110 days of gestation) was 3.62 years in females (Interquartile range, IQR = 2.9–4.3, n = 239) and 5.28 years in males (IQR = 4.2–6.3, n = 167). Reproductive tenure was defined as the time from the estimated onset of adulthood until the date of death or the end of the study, whichever came first.

Sample collection and paternity analysis

Biological samples such as tissue, hair, and feces, were collected opportunistically. Fecal samples consisted of the epithelial-rich mucus layer surrounding fresh feces, collected directly after defecation. All biological material was preserved in either ethanol or a dimethyl sulfoxide salt solution until DNA extraction. Parentage was determined using nine highly polymorphic microsatellite loci[75] with a mean of 11.9 alleles per locus (range: 7–16) and a mean expected heterozygosity of 0.83. Paternity was assigned using maximum likelihood methods as implemented in CERVUS 3.0[76] based on candidate fathers present in the natal clan at the estimated date of conception. Total exclusionary power was 0.999 and the error rate was 0.44% and set at 1.0%. Paternity was assigned at the 95% confidence level. For full methodological details, see[43] and references therein.

Data analysis

All analyses were conducted in R (version 4.5.0). Data were compiled into a centralized database and processed using the hyenaR package version 0.10.0.9000[77]. Summary statistics correspond to means ± SD, unless stated otherwise. For the statistical tests, significance was assessed at the threshold $\alpha = 0.05$. We fitted all statistical models with the package glmmTMB version 1.1.9 [78]. Model diagnostics were assessed using package DHARMa version 0.4.7[79]. ChatGPT (OpenAI) was used to assist in improving and debugging code during data analysis; all code and results were independently verified by the authors.

Reproductive success

We quantified reproductive success as: (1) the mean number of offspring produced per year during adulthood, (2) the total number of offspring produced over an individual's lifetime (LRS), and the total number of (3) grandoffspring and (4) great-grandoffspring produced. Reproductive success was assessed based on genetically confirmed parent-offspring relationships, using only cubs for which both maternity and paternity were verified through genetic analysis. Grandoffspring and great-grandoffspring were included only if they descended from such genetically confirmed offspring, ensuring consistent criteria across generations and between sexes. Mean annual reproductive success was calculated by dividing the LRS by the reproductive tenure. To avoid inflated estimates due to small denominators, we included only individuals with a reproductive tenure greater than one year in the mean number of offspring produced per year. To ensure accurate and comprehensive estimation of LRS, we included only individuals who (1) were born in a study clan, (2) initiated their reproductive career between April 12th 1996 and January 1st 2023 (the onset of monitoring of our study population and the study end date for analyses requiring complete genetic information, respectively), (3) had not been recorded to ever disperse to a clan outside the study area, and (4) had been genetically typed for parentage analyses. Our data comprised 1,187 known adult individuals. We excluded 123 individuals not born in a study clan, 66 who initiated reproduction before systematic monitoring began on April 12th 1996, 19 who dispersed to a clan outside the study area, and 16 without a genetic sample. We assigned a cohort for each individual based on the year in which they reached adulthood. We computed LRS and the other measures of reproductive success for all individuals who reached adulthood before January 1st 2011 (with the additional tenure-criterion mentioned above for annual reproduction estimates). Individuals reaching adulthood during the year 2010 constituted the most recent yearly cohort for which at least 95% of individuals had died by January 1st 2023, ensuring near-complete reproductive histories. The resulting sample included 456 potential parents with a minimum tenure of one year, included in a larger set of 492 individuals with complete or near-complete LRS information. Within this later set, 487 (98.98%) had an estimated death date by January 1st 2023, and the remaining 1.02% had near-complete lifespans. For the lifetime numbers of grandoffspring and great-grandoffspring, 11.7% of offspring (150 of 1,284) and 19.8% of grandoffspring (376 of 1,900) were still alive on January 1st 2023 and had not yet completed their reproductive careers. To ensure comparability between female and male reproductive success estimates, and to evaluate the potential impact of censored data on grandoffspring counts, we therefore assessed the overall degree of completeness in grandoffspring counts and whether it differed between the sexes (see Supplementary Information Section 1). Although absolute numbers should be interpreted with caution, great-grandoffspring counts remain suitable for female vs. male comparisons because all focal individuals reached adulthood within the same time window.

Reproductive inequality

To quantify reproductive inequality, we first used the multinomial M-index[44]. This index captures the extent to which reproductive success is unevenly distributed among a group of individuals. When all individuals are considered to have equal exposure time (e.g. the entire lifespan), the M-index reduces to the traditional metric *I* quantifying the opportunity for selection[44]. The M-index is constructed to be robust to differences in sample size and mean reproductive success, enabling standardized comparisons across populations, sexes, and species. We calculated the M-index for different measure of reproductive success: (1) the number of offspring produced per year (M_{OYear}), (2) the LRS (M_{OLife}), (3) the total number of grandoffspring produced (M_G), and (4) the total number of great-grandoffspring (M_{GG}). M_{GG} was highly skewed and to ensure numerical stability in the Bayesian estimation for this metric, we followed developer guidance for setting priors (mean = 8 ± 0.2) on the concentration term in their model and increased some of the MCMC tuning parameters (adapt_delta = 0.99, max_treedepth = 14). These adjustments minimized divergent transitions and improved convergence of the posterior estimates. All M-indices and their 95% credible intervals were calculated separately for females and males using the R package SkewCalc[44].

We also computed the Gini coefficient[80] using the Gini function from the R package DescTools (version 0.99.60)[81] and represented their associated Lorenz curves for offspring, grandoffspring, and great-grandoffspring, separately for each sex. The Gini coefficient is a widely used metric to quantify inequality that is bounded between 0 (maximum equality) and 1 (maximum inequality). For each sex, individuals were sorted by their number of descendants, and cumulative proportions of individuals and reproductive output were used to construct the Lorenz curves[45].

Maternal dominance rank at birth

Dominance hierarchies were constructed based on observed outcomes of dyadic agonistic interactions among adults in the same clan at the beginning of the study. Rankings after this initial period were updated iteratively to reflect the most consistent linear order, based on conventions such as maternal rank inheritance and social queuing and behavioral observations. For full details see[60]. We defined maternal dominance rank at birth as the ordinal position of an individual's mother in the adult female dominance hierarchy on the date of the individual's birth. Because systematic dominance data began on April 12th 1996, for individuals born between April 12th 1995 and April 12th 1996 (i.e., alive as sub-adult at the start date of the project) we used their mother's rank on April 12th 1996 as approximation for the unknown rank of their mothers at birth; the same approximation was applied when assigning standardized ranks. For a few individuals who started their reproductive career after April 12th 1996 but born before April 12th 1995, we did not assign them maternal ranks. The maternal dominance rank at birth reflects the maternal social status an individual was born into and serves as a proxy for early-life social conditions and as a proxy for privilege. For brevity, we refer to this variable as maternal rank. For visualization purposes in Fig. 2, maternal rank was further divided into categories. Specifically, we calculated the standardized maternal dominance rank, which ranges from –1 (lowest) to +1 (highest), and partitioned this continuous measure into three categories: high (0.333 to 1), medium (–0.333 to 0.333), and low (–1 to –0.333).

Sex differences in the offspring–grandoffspring relationship

We fitted statistical models to investigate the relationship between the number of grandoffspring and the number of offspring across sexes. The response variable was the number of grandoffspring produced per individual. We modelled the expected number of grandoffspring as a function of the log-transformed number of offspring, data completeness, and sex, including interactions between sex and both predictors. The number of offspring was log-transformed to linearize the relationship. The variable *completeness* corresponds to the proportion of an individual's offspring that were deceased by the end of the study. Completeness was included as a covariate to account for differences in the proportion of offspring with full record of reproductive success per individual, serving as an estimator of how complete the observed grandoffspring counts were. We ztransformed this variable to facilitate convergence during the fitting procedure. Individuals with zero offspring always have zero grandoffspring and were therefore excluded from this analysis.

Given the count nature of the data and an excess of zero values compared to Poisson expectation, we attempted to fit a series of models with different distributional assumptions: a zero-inflated Poisson Generalized Linear Model (ZIP), a negative binomial model (NB2), and zero-inflated negative binomial models (ZINB2). All these models considered the log function as their link function. We retained the ZINB2 model as this was the only one for which modelling assumptions were satisfied (as evaluated using DHARMa). For zero-inflated models (including the retained ZINB2 one), we modelled the zero-inflation component (i.e. the logistic regression sub model) with either an intercept only or with an intercept and a linear effect of completeness, as more incomplete offspring records could increase the likelihood of zeros grandoffspring. Including completeness in the formulas of the zero-inflation components improved model fits substantially, so we retained this formulation in the final ZINB2 we used. The significance of estimates was tested using a series of likelihood ratio test (LRT) following a type II Anova design using the R package car[82] which internally calls the method implemented in glmmTMB. For Fig. 2, model predictions and their associated 95% confidence intervals were plotted on the response scale, corresponding to the expected number of grandoffspring for a given offspring number at a completeness of one (mean-centered reference value).

To examine how the relationship between the number of grandoffspring and offspring varied between sexes at high reproductive output, we restricted the dataset to individuals that produced ten or more offspring. For each sex, we calculated Spearman's rank correlation coefficient (ρ) between the number of offspring and grandoffspring. Differences between female and male correlations were tested using the function diffcor.two from the R package diffcor (version 0.8.4)[83]. To assess whether maternal rank contributed to observed sex differences, we also calculated for each sex, the proportion of individuals in the subset that were born to high-ranking mothers (standardized maternal rank category = High).

Pedigree construction

We built a multi-generation pedigree for all study individuals using a combination of genetic parentage assignment and behavioral observations of suckling (consistent mother–cub associations during lactation).

Intergenerational persistence of social rank: maternal vs. paternal lineage

To test whether sex-specific differences in the intergenerational persistence of maternal rank were associated with patterns of social rank inheritance, we reconstructed genealogical lineages using the pedigree for all individuals born during the study period and with at least one known parent. We identified a total of 2,868 individuals. Of these, 2,743 had a known mother. For maternal identity, we used the socially assigned mother since we were interested in the effect of the transmission of social ranks and since cubs inherit the ranks of their social mother. In 58 cases, the social and genetic mother differed, indicating instances of adoption. Additionally, genetic data were available to assign paternity for 1,839 individuals.

The 2,743 individuals with a known mother were defined as focal individuals belonging to generation 0, G0, irrespective of birth year. For each focal individual, we calculated the maternal rank of their mother (G1), maternal grandmother (G2), and earlier ancestors along the direct maternal (social) lineage. We also reconstructed an equivalent paternal lineage and identified the maternal rank of each paternal ancestor—i.e., the focal individual's father (G1), paternal grandfather (G2), and so on. This approach allowed us to quantify and compare the intergenerational persistence of maternal rank across sexes. To avoid sparsity in the lower tail of the distribution of social ranks and facilitate comparisons across generations and sexes, we grouped individuals that were ranked 39th or below (40th, 41th...) according to their maternal ranks into one single ordinal class.

To quantify the intergenerational persistence of maternal rank among top-ranking (‘alpha’) individuals, we calculated, for each generation, the proportion of individuals whose maternal ordinal rank was equal to one. We then measured the fold-change in the proportion of alpha-ranked ancestors between successive generations. A geometric mean of these fold-changes was used to obtain a single summary statistic across all generations including 20 individuals or more to ensure reliable and informative measures.

To test whether the observed persistence of maternal rank differed from expectations under a model with rank-related fitness benefit but without rank inheritance, we performed an analysis by permutation. For each ancestor in each generation, we reassigned maternal rank by randomly selecting a mother from the same social clan and cohort window (defined as the two-year period preceding the birth of the focal ancestor). If the two-year window extended before April 12th 1995, the corresponding ancestor was excluded from the permutation analysis since no maternal rank could be inferred with precision. This permutation scheme preserved the demographic and social structure of the population, including variation in reproductive output and the elevated reproductive success of high-ranking females, but disrupted lineage continuity by breaking the parent-offspring inheritance of rank. We repeated this permutation procedure across all generations and recalculated the geometric mean of fold-changes in the proportion of alpha individuals between successive generations, for each permutation round, to generate a null distribution of the summary statistic. As before, fold changes were computed only for generations with ≥20 eligible individuals. The observed geometric mean was then compared to this null distribution to evaluate whether the persistence of high maternal rank across generations exceeded expectations under the null model. The p-value was calculated as the proportion of permuted values that were equal to or greater than the observed value, with a standard correction [84].

Long-term genetic contribution

For each focal individual, we quantified their genetic contribution as the expected number of copies of their alleles present in the population as of January 1st 2023. For each focal individual *i* we calculated g_i, defined as the sum of pedigree-derived pairwise relatedness coefficients to all known descendants of *i* that were alive at that date:

$$g_i = \sum_{j=1}^{n} r_{ij},$$

where r_{ij} is the coefficient of relatedness between focal individual i and the descendant j as calculated from the pedigree, and n is the number of recorded descendants alive at the end date.

To examine how well simple reproductive counts capture genetic representation, we calculated Spearman correlations between g_i and the number of offspring and grandoffspring for each adult individual included in the reproductive inequality analysis. Because the pedigree used to count descendants incorporated behavioural observations, we also considered offspring whose mothers were assigned behaviorally or genetically without assigned fathers, relaxing the stricter criteria used in the reproductive-success analyses. Correlation analyses included only individuals with at least one offspring, resulting in a sample size of 406 adults.

Share of descendants for most successful females

We analyzed females with the highest number of living descendants as of January 1st 2023. This analysis included all adult females known during the study period. Using the pedigree of the population, we counted each female's total number of unique descendants and determined which of those were alive at the target date. For each female, we recorded: (1) total number of descendants, (2) number of descendants alive, and (3) number of living descendants that were present in the female's natal clan on January 1st 2023. We then identified, within each clan, the female with the highest number of living descendants. For each of these most successful females, we determined if they ever reached the alpha position during their lifetime, and we recorded their year of death. To provide context on lineage persistence, we calculated the proportion of each female's living descendants that remained in her natal clan relative to the total number of native individuals alive in that clan, regardless of whether their ancestry was fully known or not. Clan size estimated for January 1st 2023 is also reported and includes both native individuals and immigrant males.

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Author Contributions

Conception: M.M., A.C., O.P.H., and E.D; Methodology: M.M., A.C., O.P.H., and E.D; Investigation: M.M., O.P.H, E.D, and P.N; Data curation: O.H. and P.N.; Formal analyses: M.M. and A.C; Visualization: M.M. and A.C.; Original draft: M.M.; Validation: A.C. and O.P.H.; Reviewing and editing: A.C., O.P.H and E.D.; Supervision and administration: E.D. and O.P.H.; Funding acquisition: O.P.H.

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Supplementary Information

Contents:

Supplementary Information S1: Completeness of grandoffspring counts across sexes

Because our reproductive success metrics included the number of grandoffspring, we evaluated how complete these counts were for each focal individual. We use the term "completeness" to refer to the degree to which an individual's grandoffspring count could be considered complete at the end of the study period. This depends on whether their genotyped offspring had died—and thus had uncensored opportunities to reproduce—or were still alive and potentially reproducing beyond the study's end. Incomplete grandoffspring counts may thus underestimate multigenerational reproductive success.

To test for potential sex-specific biases in data completeness, we first compared the proportion of individuals with no surviving offspring between females and males using a Fisher exact test. Among individuals with at least one surviving offspring, we compared the number living offspring between sexes using a Wilcoxon rank-sum test. Finally, we calculated an individual-level completeness score, defined as the proportion of an individual's offspring that were deceased by the end of the study. Individuals with no offspring were assigned a score of 1.0 (fully complete).

Of all selected individuals (n = 492), 77.4% had no offspring alive at the end of the study period: 79.8% (n = 229 out of 287) of females and 74.1% of males (n =152 out of 205). This difference was not significant (Fisher's exact test; odds ratio = 0.727, 95% CI: 0.465–1.14, p = 0.155). Among individuals with at least one living offspring (n = 111), the number of living offspring did not differ significantly between sexes (Wilcoxon rank-sum test: W = 1,363, p = 0.258). Completeness scores were generally high (mean = 0.932, SD = 0.162). Females (mean = 0.944, SD = 0.135) and males (mean = 0.914, SD = 0.192) completeness scores did not differ significantly (Wilcoxon rank-sum test: W = 31,220, p = 0.113).

Supplementary Information S2: Mean reproductive tenure in females and males

The mean reproductive tenure was significantly higher in females (7.31 ± 4.34 years; range = 0.002–16.46; n = 287) than in males (6.45 ± 3.66 years; range = 0.109–15.30; n = 205; Wilcoxon rank-sum test: W = 32,684 , p = 0.0356). Among individuals with a minimum tenure of one, mean reproductive tenure was also significantly higher in females (7.80 ± 4.08 years; range = 1.07–16.46; n = 268) than in males (6.99 ± 3.36 years; range = 1.03–15.30; n = 188; Wilcoxon rank-sum test: W = 27,993, p = 0.043).

Sex	Offspring rate	Offspring	Grandoffspring	Great-grandoffspring
female	0.400	0.517	0.762	0.88
male	0.448	0.514	0.659	0.82

Supplementary Table S1 | Gini coefficients for reproductive success in female and male spotted hyenas.

Gini coefficients quantify inequality in four measures of reproductive output: (i) offspring production rate, calculated from individuals with >1 year of reproductive tenure; and (ii) total number of offspring, grandoffspring, and great-grandoffspring. Gini coefficients range from 0 (perfect equality) to 1 (maximum inequality). While males exhibit greater inequality in offspring production rates, inequality in lifetime offspring counts is similar between the sexes. Across generations, however Gini values increase, particularly among females, indicating that reproductive success becomes increasingly concentrated within a small number of individuals.

Gini coefficients were calculated using the DescTools package. Note that the offspring production rate is not directly comparable to the M_{OYear}, because it was restricted to individuals with a minimum reproductive tenure of >1 year to ensure meaningful annual rate estimates, whereas the M_{OYear} includes all individuals regardless of tenure since the M-index computation accounts for differences in tenure.

Component	Term	Estimate	SE	chisq	df	p-value
cond	Intercept	-0.099	0.197			
cond	Sex (male)	0.877	0.266	2.687	1	0.101
cond	Log number of offspring	1.472	0.107	258.382	1	< 0.001
cond	Completeness	0.072	0.073	0.290	1	0.59
cond	Sex (male) × Log number of offspring	-0.424	0.144	8.623	1	< 0.01
cond	Sex (male) × Completeness	-0.079	0.095	0.696	1	0.404
zi	Intercept	-24.191	3,966.872			
zi	Completeness	46.893	8,168.936			

Supplementary Table S2 | Parameter estimates from the zero-inflated negative binomial (ZINB) model of grandoffspring count. Results are shown separately for the conditional (count) and zero-inflation components. Estimates are presented on the model link scale (log for the count component, logit for the zero-inflation component). Likelihood-ratio test (χ^2) statistics and associated p-values are reported in place of z-tests.

Sex	N	Mean	Median	SD	Min	Max	25th %ile	75th %ile
Female	239	1.418	0.262	2.789	0	24.109	0	1.672
Male	167	1.941	1.000	2.525	0	12.875	0	2.692
All	406	1.633	0.609	2.693	0	24.109	0	2.100

Supplementary Table S3 | Descriptive statistics of expected genetic contribution for all individuals and separated by sex.

Supplementary Figures

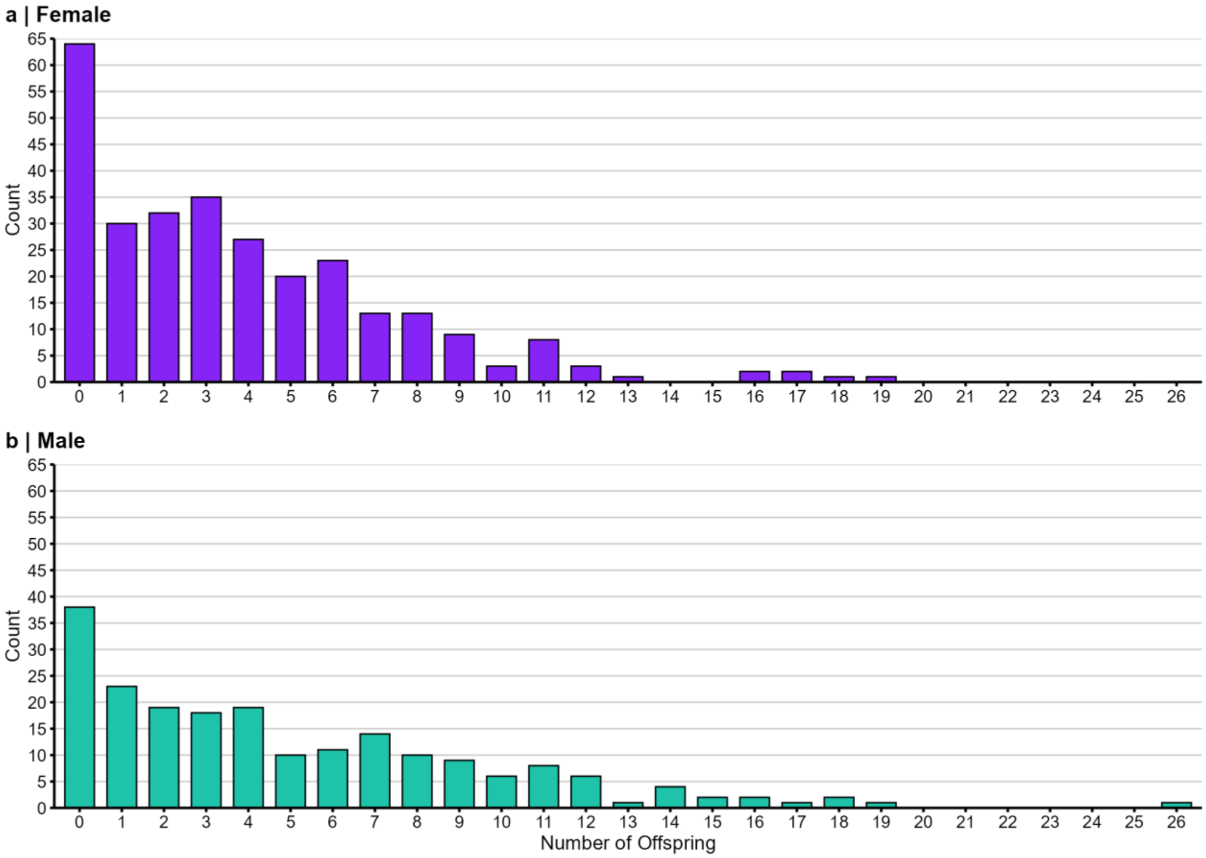

Fig. S1 | Frequency distributions of lifetime reproductive success in female and male spotted hyenas.

Number of offspring produced (a) by females (n = 287) and (b) by males (n = 205). Lifetime reproductive success was defined as the total number of offspring produced by each individual.

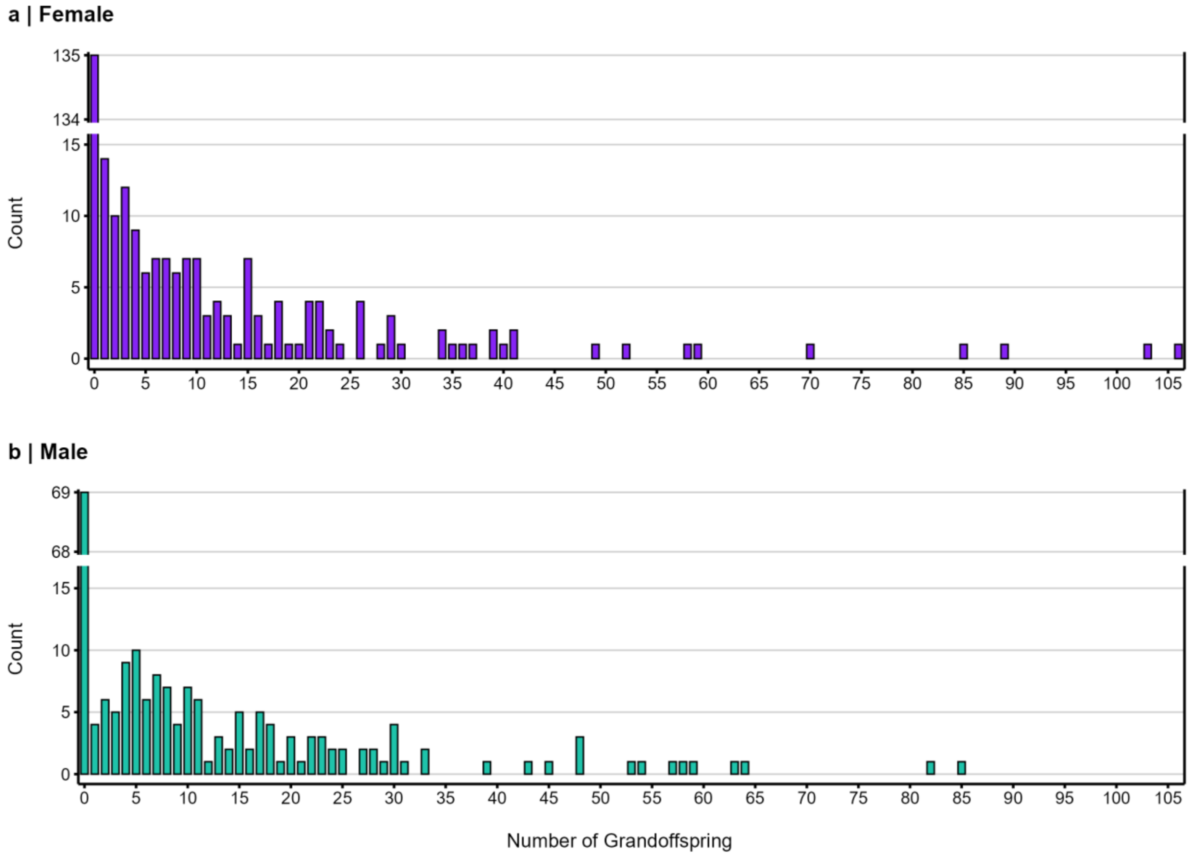

Fig. S2 | Frequency distributions of grandoffspring counts in female and male spotted hyenas.

Number of grandoffspring produced (a) by females (n = 287) and (b) by males (n = 205). Y-axis breaks were used to improve readability given the high frequency of individuals with zero grandoffspring.

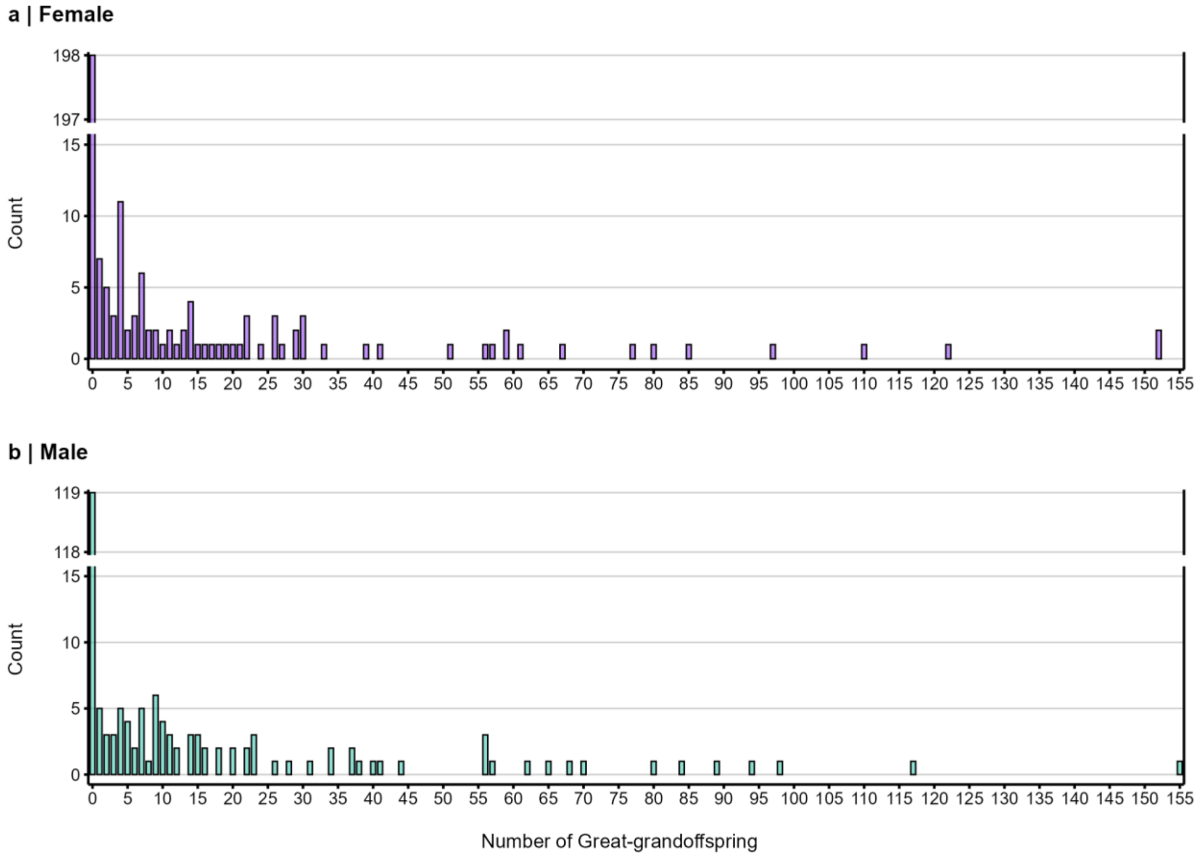

Fig. S3 | Frequency distributions of great-grandoffspring counts in female and male spotted hyenas.

Number of great-grandoffspring produced (a) by females (n = 287) and (b) by males (n = 205). Y-axis breaks were used to improve readability given the high frequency of individuals with zero great-grandoffspring.

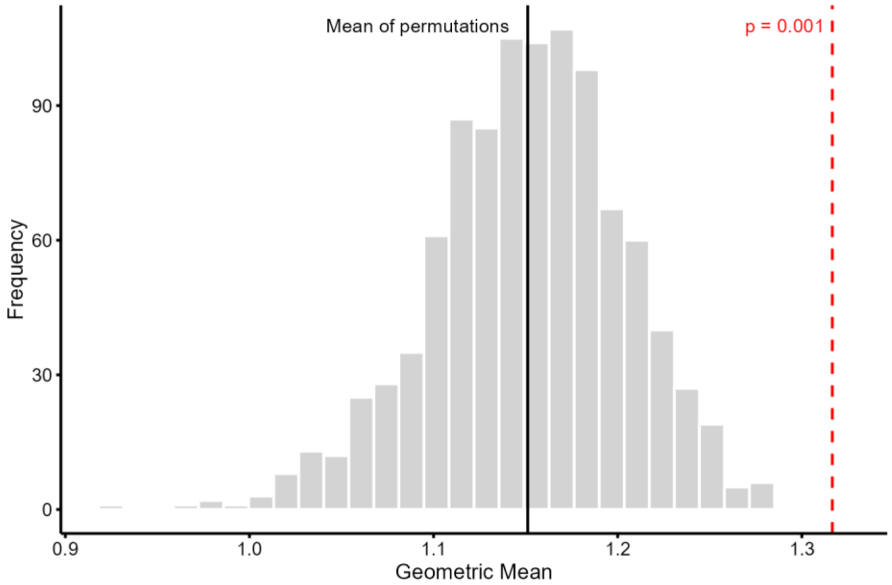

Fig. S4 | Permutation distribution of geometric means for maternal-line rank transmission. The histogram shows the distribution of geometric means across permutations of maternal identity within clans and two-year retrospective birth cohorts, under a null model excluding social rank inheritance. The solid black line indicates the mean of the permutation distribution, and the dashed red line marks the observed geometric mean from the actual maternal lineages. The observed value lies near the upper tail of the null distribution, suggesting that the intergenerational continuity in rank is stronger than expected by chance. The corresponding permutation p-value is displayed on the plot.