nature ecology & evolution

ARTICLES

https://doi.org/10.1038/s41559-018-0718-9

Social support drives female dominance in the spotted hyaena

Colin Vullioud[1,2,4], Eve Davidian[1,4], Bettina Wachter[1], François Rousset[3], Alexandre Courtiol[2,4] and Oliver P. Höner[1,4]*

Identifying how dominance within and between the sexes is established is pivotal to understanding sexual selection and sexual conflict. In many species, members of one sex dominate those of the other in one-on-one interactions. Whether this results from a disparity in intrinsic attributes, such as strength and aggressiveness, or in extrinsic factors, such as social support, is currently unknown. We assessed the effects of both mechanisms on dominance in the spotted hyaena (*Crocuta crocuta*), a species where sexual size dimorphism is low and females often dominate males. We found that individuals with greater potential social support dominated one-on-one interactions in all social contexts, irrespective of their body mass and sex. Female dominance emerged from a disparity in social support in favour of females. This disparity was a direct consequence of male-biased dispersal and the disruptive effect of dispersal on social bonds. Accordingly, the degree of female dominance varied with the demographic and kin structure of the social groups, ranging from male and female co-dominance to complete female dominance. Our study shows that social support can drive sex-biased dominance and provides empirical evidence that a sex-role-defining trait can emerge without the direct effect of sex.

Dominance relationships within and between the sexes shape female and male reproductive strategies, define sex roles and drive key evolutionary processes, such as sexual selection and sexual conflict[1–3]. In many species, members of one sex dominate those of the other in one-on-one ('dyadic') interactions[4–6], yet the proximate mechanisms that lead to such sex-biased dominance are poorly understood[7–9]. The prevailing hypothesis posits that one sex dominates the other when it is superior in intrinsic attributes, such as physical strength or aggressiveness[10]. This has been proposed to explain why in many species males are the dominant sex[4,5]. However, recent studies showed that intrinsic attributes fail to account for the wide variation in sex-biased dominance observed in primates, including humans[8,11]. In primates and social species of other taxa, such as carnivores and birds, the outcome of dyadic interactions might also be influenced by social support; individuals with greater social support may be more assertive and more likely to win an encounter, even when their coalition partners are absent or do not intervene[12–14]. Whether such indirect social support influences dominance relationships between females and males and causes sex-biased dominance has not been tested empirically in any animal.

In this study, we investigated the extent to which intrinsic attributes and social support predict dominance both within and between the sexes in the spotted hyaena, *C. crocuta*. Spotted hyaenas are large carnivores that live in clans structured by a linear dominance hierarchy[15]. The highest rank in the clan is usually occupied by a female and the social system of spotted hyaenas has been viewed as an archetype of a female-dominated and sex-role-reversed system[16,17]. Sexual size dimorphism is low and only detectable in some morphological traits; adult females are less than 3% longer, less than 1% taller and approximately 10% heavier than adult males[18] (a characteristic also shown in this study). Previous studies proposed that females became dominant by evolving into the larger and more aggressive sex[15,16]. However, these studies did not consider the potential effects of social support and focused on social contexts where the effects of social support and sex are confounded[19].

Results and discussion

We monitored the outcome of agonistic, dyadic interactions ($n = 4{,}133$) between 748 hyaenas from eight clans inhabiting the Ngorongoro Crater, Tanzania. We assessed the effects of body mass (as a proxy for physical strength), sex (as a proxy for any other sex-related intrinsic attribute, such as aggressiveness) and social support on the outcome of these interactions. We observed interactions between individuals of the same and different sex in four social contexts: 'interclan', when two individuals of different clans interacted and one or both individuals were outside their clan territory ($n = 502$); 'intraclan-mixed', when a native individual interacted with a male that had immigrated to the clan ($n = 601$); 'intraclan-native', when both were natives of the same clan ($n = 1{,}801$); 'intraclan-immigrant', when both were males that had immigrated to the same clan ($n = 1{,}229$). Immigrants were always males because female hyaenas rarely disperse[20,21]. Studying the outcomes of agonistic interactions in these contexts allows us to tease apart the intrinsic attributes and social support hypotheses because the predictions differ between the contexts (Supplementary Tables 1 and 2). Interclan interactions are particularly useful to disentangle the effects of sex-related intrinsic attributes and social support because males can have more or less social support than females depending on where the interaction takes place.

We estimated indirect social support, defined as the number of hyaenas who could be recruited and would provide support for each interacting individual by three quantitative proxies depending on the social context: (1) for interclan interactions, the proximity to the core area of activity of each individual's respective clan ('supporter proximity'); (2) for intraclan-immigrant interactions, the

---

[1]Department of Evolutionary Ecology, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. [2]Department of Evolutionary Genetics, Leibniz Institute for Zoo and Wildlife Research, Berlin, Germany. [3]Department of Evolutionary Genetics, ISEM, Université de Montpellier, CNRS, IRD, EPHE, Montpellier, France. [4]These authors contributed equally: Colin Vullioud, Eve Davidian, Alexandre Courtiol, Oliver P. Höner *e-mail: hoener@izw-berlin.de

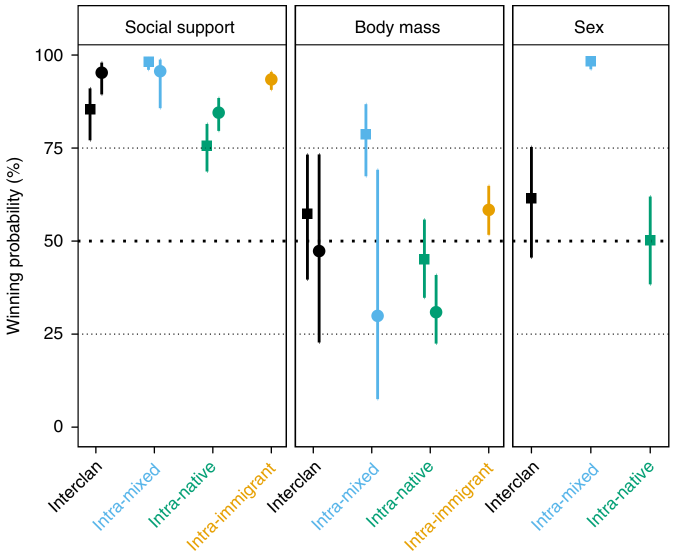

Fig. 1 | The effect of social support, body mass and sex on the probability that a spotted hyaena wins a dyadic interaction. Winning probabilities are predicted probabilities ±95% CI for the four social contexts: interclan (members of two different clans interact), intra-mixed (native female or male interacts with immigrant male of the same clan), intra-native (two natives of same clan interact), intra-immigrant (two immigrant males of the same clan interact); and the two sexual contexts: intersex (female interacts with male, depicted with filled squares) and intrasex (two individuals of the same sex interact, depicted with filled circles). Probabilities were predicted for the individual with the greater social support ('social support' box), the heavier individual ('body mass' box) and the female ('sex' box).

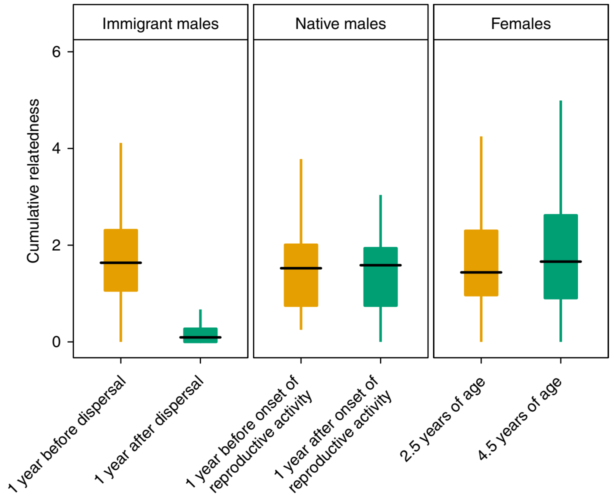

Fig. 2 | The effect of dispersal and age on the cumulative relatedness of spotted hyaenas. Cumulative relatedness is the sum of relatedness coefficients between an individual and all other clan members calculated through the maternal lineage. For immigrant males ($n=222$), cumulative relatedness was calculated 1 year before and after dispersal; for native males ($n=33$), 1 year before and after the onset of reproductive activity; and for females ($n=372$), 1 year before and after the mean male dispersal age of 3.5 years[21]. The boxes indicate the interquartile range around the median (horizontal bar) and the vertical bars represent the cumulative relatedness values that lie within 1.5 times the interquartile range.

time since the immigrant's arrival ('tenure'); (3) for intraclan-mixed and intraclan-native interactions, the 'number of supporters' as estimated by an algorithm based on decision rules derived from previously established patterns of social support and a detailed genetic pedigree spanning 21 years and eight generations (see Methods and Supplementary Fig. 1). We used generalized linear mixed-effects models (GLMMs) to predict the outcome of interactions based on the difference in social support, body mass or sex between the two individuals.

In accordance with the social support hypothesis, the winning probabilities predicted by social support were high (between 76 and 98%) in all social contexts and for both intersex and intrasex interactions (Fig. 1, 'social support' box and Supplementary Table 3). In contrast, the effects of intrinsic attributes were inconsistent across social contexts (Fig. 1, 'body mass' and 'sex' boxes) and opposite for intersex and intrasex interactions in two out of three social contexts (Fig. 1, winning probabilities >50% versus <50% in 'body mass' box). In addition, model comparison based on the Akaike information criterion (AIC) and Tjur's *D* showed that the predictive powers of all models considering social support were substantially higher than those of the other models (Supplementary Table 4).

Intrinsic attributes only seemed to influence the outcome of intraclan-mixed interactions between females and immigrant males (Fig. 1, filled blue square in the 'sex' box and Supplementary Table 3). However, in this social context, the effects of social support and sex are confounded because females interact with males who have less social support; in spotted hyaenas, social support is mostly given to kin[22] and immigrant males have few or no relatives (Fig. 2 and Supplementary Fig. 2). Where the two effects can be disentangled, the effect of sex-related attributes is negligible; native males were as likely as native females to win against immigrant males (Fig. 1, filled blue square and circle in the 'social support' box) and native females had a winning probability of only 50% against native males (Fig. 1, filled green square in 'sex' box).

Female dominance over immigrant males may also result from reproductively active males conceding dominance to females to achieve mating ('docile male hypothesis')[9,23] or dispersing males experiencing an 'ontogenetic switch' that makes them submit to natives on immigration[19,24]. Our results are inconsistent with the docile male hypothesis because immigrant males were as likely to lose against native males and females (Fig. 1, filled blue square and circle in 'social support' box), and native males that were reproductively active dominated females (Supplementary Fig. 3), including females they sired offspring with. To disentangle the effect of social support from a possible ontogenetic switch associated with immigration status, we analysed the outcome of interclan interactions between natives of both sexes and immigrant males ($n=153$ interactions, including 60 with females). We found that immigrant males who had greater social support, that is, who were closer to the core area of activity of their new clan, had a 97% winning probability (95% confidence interval (CI) = 85–99%). This confirms that asymmetries in social support had a much stronger influence on the outcome of interactions than ontogenetic processes. Our results are also unlikely to be confounded by differences in residency, age or self-organizing processes, such as winner–loser effects (see Supplementary Notes).

Our results show that dominance between two spotted hyaenas is primarily established by asymmetries in social support, both within and between the sexes. They also show that female spotted hyaenas only consistently dominated males who had immigrated into their clan, that is, males who had lost their social bonds during dispersal. The disruptive effect of dispersal on social bonds and the importance of social support for dominance imply that the degree of female dominance should vary with the strength of the sex bias in dispersal and the demographic and kin structure of the social groups, in particular, the ratio of natives to immigrants and

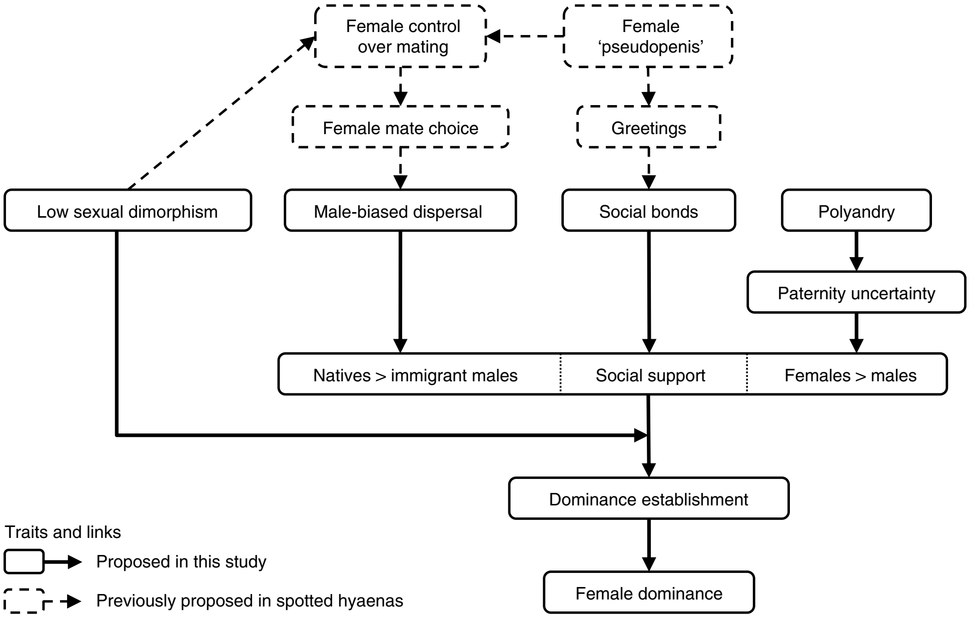

Fig. 3 | The emergence of female dominance in spotted hyaenas and other social species. In species with low sexual dimorphism in size, strength and aggressiveness, social support can have a stronger influence on dominance establishment than individual intrinsic attributes. Male-biased dispersal influences the demographic and kin structure of social groups and reduces social support of immigrant males. Polyandry can further reduce social support of males compared with females by inducing paternity uncertainty[59] and reducing paternal investment and social bonding between fathers and their offspring[1]. When sexual dimorphism is low, this disparity in social support in favour of females can mediate female-biased dominance.

the relatedness among immigrants. Accordingly, female dominance in our study population, calculated using the standardized Mann–Whitney *U*-test statistic of female and male social ranks[8], ranged from 0.5 (female and male co-dominance) when the ratio of native males to immigrant males was high, to 0.98 (nearly complete female dominance) when a clan contained mostly native females and immigrant males unrelated to one another (Supplementary Table 5).

Studies on various taxa have shown that social support serves as a means to reinforce intrasexual dominance relationships within already established social hierarchies[22,25]. In this study, we show that social support can actually be the basis from which social hierarchies emerge. Social hierarchies are usually derived based on the proportion of wins of each group member against the other group members in dyadic interactions[26]. We showed that individuals with greater social support won, overall, more than 80% of their interactions (Supplementary Table 3). As a result, all group members are ultimately ranked according to their relative number of supporters. Once hierarchies are established, social support (as well as winner–loser effects) may help reinforce dominance relationships between group members because high-ranking individuals recruit more offspring than lower-ranking individuals[27], which reinforces asymmetries in the number of supporters[22]. The importance of social support for social dominance may favour the emergence of behavioural tactics to manipulate asymmetries in social support. Adoptions and infanticide by females observed in many group-living species[28,29], including spotted hyaenas[30,31], may represent such tactics; adoptions increase the surrogate mother's number of future coalition partners while reducing that of the biological mother; infanticide reduces the number of future coalition partners of the infant's mother[32].

Our finding that body mass and sex had only minor effects on the outcome of interactions contradicts the intrinsic attributes hypothesis and the view that female spotted hyaenas achieved dominance by becoming the larger and more aggressive sex[15–17]. It shows that factors other than sexual dimorphism in size, strength and aggressiveness can be the main determinant of the emergence of sex-biased dominance (see also Hemelrijk et al.[8]). We propose that low sexual dimorphism reduces power asymmetries between the sexes and thereby promotes alternative pathways to dominance establishment, such as the pathway involving social support demonstrated in this study (Fig. 3). Male-biased dispersal and polyandry can both induce a disparity in social support in favour of females and play a key role in the emergence of female dominance (Fig. 3). Fluctuations in the demographic structure of social groups, including the sex ratio, ratio of natives to immigrants and the relatedness among immigrants, may contribute further to the wide variation in the degree of sex-biased dominance within and between group-living species[6,8].

Our study demonstrates that social support can mediate sex-biased dominance. Although shown in this study for a system with female-biased dominance, disparities in social support between the sexes may also drive male-biased dominance. Our study further provides empirical evidence that sex-role-defining traits may not be directly caused by sex determination but can emerge from differences in the ecology and life history between males and females[33,34]. It also shows that sex-role-defining traits can vary depending on the social and breeding systems and the demographic structure of the social units[35].

Methods

Spotted hyaenas. Spotted hyaenas live in clans of up to 130 members. Clan social structure is characterized by a stable linear dominance hierarchy[15]. Offspring of both sexes acquire a social rank just below that of their mother through behavioural support and social learning ('maternal rank inheritance')[31,36]. They then build social bonds with other clan members, the strongest of which are with close relatives[22]. Rank reversals are rare and only occur during 'coups' when a coalition of lower-ranking members dethrone a higher-ranking coalition[37]. Immigrant males join the new clan at the bottom of the hierarchy, usually only increase in rank with increasing tenure in the clan when a higher-ranking clan member dies or disperses and remain subordinate to all native clan members[21,38]. Spotted hyaenas live in 'fission–fusion' societies in which clan members often spend time alone or in small subgroups[37,39]. They frequently undertake excursions to areas outside the territory boundary of their clan and interact with hyaenas from other clans; both intraclan and interclan interactions often involve only two individuals[20,40].

Study population. We monitored all hyaenas of the eight resident clans inhabiting the 250-km^2 floor of the Ngorongoro Crater (3° 11′ S, 35° 34′ E) in Tanzania between April 1996 and December 2017; all hyaenas were individually known by their spot pattern and other cues[41]. Dispersal in this population is strongly male-biased, with approximately 85% of males and 1.5% of females leaving their natal clan and immigrating into another clan or founding a new clan in a vacated area[20,21]. Males were considered to be reproductively active in their natal clan or to have immigrated into a clan when they expressed sexual behaviour towards females of their natal clan or another clan, respectively, for at least three months[21]; the date of clan choice was the date of first observation of such behaviour for native males and of first sighting in the new clan's territory for immigrant males. The population is genetically linked to neighbouring hyaena populations outside the Ngorongoro Crater through male dispersal[20].

Social interactions. We recorded dyadic interactions between males and females within and outside their clan territory ad libitum and during focal follows. We focused on dyadic rather than polyadic interactions because in polyadic interactions, the winning probability will not only be influenced by intrinsic attributes or indirect social support but also by other factors, such as the size of the two interacting parties. In addition, social ranks and dominance hierarchies in social groups are typically derived from the outcome of dyadic rather than polyadic interactions[26]. The winner of an interaction was determined based on aggressive actions (lunging, chasing, biting, pushing) and submissive reactions (retreating, cowering, ears down, tail between legs)[42]. Of a total of 5,783 interactions with unambiguous outcomes between individuals older than 1 year of age, we analysed 4,133 interactions, including 502 interclan, 601 intraclan-mixed, 1,801 intraclan-native and 1,229 intraclan-immigrant interactions. Interclan interactions took place in the clan territory of one of the interacting individuals or a third clan's territory. We restricted the analyses to interactions between individuals older than 1 year of age (mean ± s.d. = 5.74 ± 3.13 years, maximum = 19 years) because dominance relationships among younger hyaenas are unstable and the outcome of their interactions depends on maternal intervention, that is, direct social support[43]. Juveniles may still be learning social conventions (dominate or submit to others) and being introduced to clan members, including potential supporters. The 1,650 interactions that we excluded from the analyses were: (1) interactions for which one of the covariates could not be computed due to missing information ($n = 1{,}167$); (2) interactions involving an immigrant male and a member of his natal clan ($n = 288$) because it is unknown for how long males that dispersed from their natal clan benefit from social support by members of their natal clan[41]; (3) interactions involving female dispersers ($n = 64$ interactions involving 4 females) and males that had immigrated into a clan and then re-dispersed back into their native clan ($n = 6$) due to small sample sizes. We also excluded interactions between twins or descendants of twins ($n = 125$) because it is currently unknown which of two twins are supported by other clan members. Previous studies showed that dominance relationships between young twins may be reinforced by winner–loser effects[44], but the determinants of dominance establishment between twins (for example, biased maternal social support or asymmetry in body mass arising from birth order[45,46]) remain largely unknown.

Relatedness. Relatedness and ancestry were based on extensive genetic pedigree information (2,132 maternal links and 1,367 paternal links) across 8 generations. Calculation of relatedness coefficients was based on the maternal lineage because spotted hyaenas only very rarely build coalitions along the paternal lineage[22]. Genetic samples for parentage assignments were collected and processed as previously described[20,47] and parentage assignments were performed using maximum likelihood methods as implemented in CERVUS version 3.0[21,48]. The total exclusionary power of assignments (0.999) and the success rate (97.2% of 1,447 sampled offspring at the 95% confidence level) were very high.

Social support. We quantified the amount of social support an individual can expect to receive using quantitative proxies derived from studies on social bonding, social networks and direct social support in spotted hyaenas. Each proxy was developed independently of pre-established dominance relationships or social ranks. For interclan interactions, we used the distance between the geographic coordinate of the encounter and the current core area of activity of the individual's clan. This considers that hyaenas recruit clan members when challenged by hyaenas from other clans by emitting long-distance calls[42], and that during encounters between residents and non-residents, the group sizes of non-residents are smaller than those of residents[40]. An analysis of polyadic interclan interactions involving 506 interacting parties in our study population confirmed that the proxy supporter proximity accurately reflects patterns of direct social support in the interclan context: the odds of getting direct support from at least one clan member decreased by a factor of 0.62 (95% CI = 0.55–0.69) when the distance to the clan's current core area of activity increased by 1 km, a distance that corresponds to one-third of the s.d. of the observed difference in distances (Supplementary Fig. 4). Furthermore, the interacting party that was closer to the clan's current core area of activity was the larger in 82% of cases ($n = 228$ interactions with information about the distances of both interacting parties and a difference in party size), the larger of the two interacting parties won in 98% of cases ($n = 249$ interactions with a difference in party size) and the interacting party that was closer to the clan's current core area of activity won 84% of interactions ($n = 243$ interactions with information about the distances of both interacting parties). The current core area of activity of a clan was defined as the average geographic coordinate of all sightings of adult females during the three months preceding the interaction date. If fewer than 20 sightings were recorded during a 3-month period, the average was computed on the 20 sightings with the smallest time difference to the date of interaction. Geographic coordinates were recorded with standard global positioning system devices (Garmin GPS III Plus and Garmin GPSMAP 60CSx; Garmin). We used the clan's current core area of activity rather than a measure related to the territorial boundaries because the current core area of activity takes into account the frequent and substantial changes in the intensity at which clan members use areas within the territory (for example, due to changes in prey distribution and the location of the communal dens used by adult females) and situations when hyaenas temporarily shift their activity to areas outside the clan territory[49,50]. Furthermore, in contrast to proxies based on territorial boundaries, using supporter proximity also allows testing for the effect of social support in areas outside the territories of the two interacting individuals and in areas where their territories overlap. The mean difference between the distances of the two individuals to their respective clans' current core areas of activity was 4.16 ± 2.94 km ($n = 502$).

For intraclan-mixed and intraclan-native interactions, we calculated for both individuals the number of potential supporters within the clan on the date of the interaction based on five main decision rules that we derived from well-established behavioural observations in spotted hyaenas and cercopithecine primates with coalition patterns and social systems very similar to those of spotted hyaenas. We combined these into an algorithm that can be adapted to other species and social systems (Supplementary Fig. 1): (1) a mother supports the younger of two of her offspring and any of the younger offspring's descendants ('youngest ascendancy')[36]; (2) a bystander supports the individual to which it is most closely related[22]; (3) a bystander supports natives of its natal clan over non-natives[22]; (4) a bystander supports the individual supported by the most recent common female ancestor of the bystander and the two interacting individuals[51]; and (5) a bystander remains neutral if the most recent common female ancestor of the bystander and the two interacting individuals is less likely to support the bystander than the two interacting individuals[51]. Rules (4) and (5) were derived from the observations that hyaenas associate and form social bonds when they already share a social partner ('the friend of my friend is my friend'), mothers are key social partners in shaping clustering patterns ('inheritance of maternal social network')[51] and bystanders adjust their decision to their competitive ability relative to that of the interacting individuals[22,25]. Because this algorithm is based on rules involving kinship, the difference in potential social support between two interacting individuals was positively correlated to their difference in cumulative relatedness (Pearson's $r = 0.62$, 95% CI = 0.60–0.65, $n = 2{,}402$; Supplementary Fig. 5); this is consistent with previous findings suggesting that individuals with more kin have more supporters than individuals with fewer kin[22]. When calculating the number of potential supporters, all clan members older than 1 year of age were considered as potential bystanders. Kinship and ancestry relationships were derived from genetic pedigree information. Cubs that were adopted (2% of 2,065 cubs) were considered as offspring of the surrogate mother. This considers that adoptees receive the social support of their surrogate mother and obtain the social rank just below that of their surrogate mother[31].

For intraclan-immigrant interactions, we used the period between the date of clan choice and the date of the interaction (tenure). This considers that immigrant males progressively foster social bonds with other males and increase the rate at which they form coalitions with other males[38]. The mean difference in tenure between two interacting immigrant males was 1.96 ± 2.13 years ($n = 1{,}229$).

For each dyad, the individual that was closer to the core area of activity of its clan (interclan interactions), had more supporters (intraclan-mixed and intraclan-native interactions) or had the longer tenure (intraclan-immigrant interactions), respectively, was considered to have greater social support.

Intrinsic attributes. The body mass of hyaenas involved in an interaction was deduced from the growth curves estimated from the body mass measurements of 77 females ($n = 1{,}558$) and 90 males ($n = 1{,}530$) aged between 1 month and 13 years using an electronic scale[52]. Because body mass is influenced by the amount of food in the digestive system, belly distension was rated as thin, thin-to-normal, normal, normal-to-full, full, full-to-bloated and bloated. We fitted an additive model to measurements rated as normal using the *gam* function of the *mgcv*[53] package, with sex and age as predictors (adjusted $r^2 = 0.93$; Supplementary Fig. 6). This model was then used to estimate the body mass of all individuals involved in the interactions included in this study, based on the individual's age on the day of the interaction and assuming that individuals followed the mean growth curve of their sex. Adult females (mean = 56.68 ± 6.24 kg) were approximately 10% heavier than adult males (mean = 51.65 ± 3.38 kg). Individuals were sexed using the shape of their phallic glans[54]. Age was determined on the basis of pelage, body size, locomotory abilities, behavioural development, and the position, shape and size of ears when they were cubs[41]; adults were 24 months of age or older.

Statistical analysis. All analyses were performed in R version 3.5.1[55]. We fitted GLMMs using the *fitme* function of the *spaMM* package version 2.5[56]. We fitted GLMM logistic regressions to predict winning probabilities of individuals using penalized quasi-likelihood[56] (using the *method* = 'PQL' option for the computation of parameter estimates and predictions, and the *method* = 'PQL/L' option for the computation of log-likelihood, AIC and Tjur's *D*)[57]. We assessed the effect of body mass, sex and social support in a series of nested models (Supplementary Table 4). Three series of models were fitted on interactions between individuals of a different sex ($n = 1{,}109$; for social support, body mass and sex) and two series of models were fitted on interactions between individuals of the same sex ($n = 3{,}024$; for social support and body mass only). Fitting interactions within a sex allows for an assessment of body mass and social support that is not confounded by differences in these covariates between the sexes.

One additional model was fitted to disentangle the effects of social support and immigration status (ontogenetic switch) on winning probability. This model was fitted on a subset of data in the interclan context that consisted of interactions between immigrant males that were closer to the core area of their clan and thus had greater social support, and native individuals.

All these models considered as focal individual the individual that was predicted to win under the respective hypothesis, that is, the individual with greater social support, the heavier individual or a female. All fixed-effect predictors (except *social_context*) were considered as binary variables indicating whether the focal individual was more socially supported (*social_support_bin*) or heavier (*body_mass_bin*) than the other individual or a female (*sex*). To account for possible dependence between interactions involving the same individual(s) in the same social context, we considered the identity of the two individuals interacting as a random effect with the following correlation coefficients between each pair of dyadic interactions: 0 (no correlation), when the two interactions involved four different individuals; +0.5 or −0.5 (intermediate correlation), when only one individual was involved in the other interaction; and +1 or −1 (perfect correlation), when the same individuals were involved in the other interaction. Positive or negative correlation was applied depending on whether the common interactor(s) maintained their position as focal/non-focal individual in both interactions or swapped position between interactions, respectively. We considered interactions involving the same individual in different social contexts as distinct information because the social support of a given individual is likely to change according to the social context. Accounting for the identity of individuals as a random effect also allowed us to control for any intrinsic differences in competitive ability between individuals other than the ones considered and tested for in each model (such as winner–loser effects or possible residual effects of dominance ranks not accounted for by our predictors).

Note that the response variable, that is, the outcome of the interaction for the individual predicted to win, differed across the series of models. The more conventional approach (when not dealing with dyadic interactions) is to compare models with the same response variable. When analysing dyadic interactions and considering multiple predictor variables, a given individual has to be considered the focal individual in each interaction. Selecting focal individuals randomly is problematic because the fits to such constructed datasets ignore the logical constraints of the dyadic interactions. For example, in intersex interactions, the fitted winning probabilities of males and females would not necessarily sum to 1 and in an extreme case where only females were sampled, no information about male parameters would be available.

In contrast, our analyses enforce the necessary constraints because they are likelihood fits of the response for only one of the partners under models consistent with the assumption that the other half of the response is fully determined by the first half. The conditional likelihood for the latter half of the response is thus 1, so that these fits provide full-data log-likelihoods, despite apparently considering different subsets of the response. For this reason, identical log-likelihoods are obtained for fits of models sharing the same variables, irrespective of which of these variables is taken as the response (Supplementary Table 4). In Fig. 1, we present the effects of the three predictors (social support, body mass and sex) on the outcome of the interaction when they were considered alone. In Supplementary Table 4, we present the results of the complete analysis; this allows for the study of the joint effect of each predictor. In Supplementary Table 6, we provide the detailed summary output of the fit of a full model.

Model predictions were computed by excluding the realization of the random effect (using the *re.form* = NA option in the *predict.HLfit* function). This ensured that our predictions did not include any intrinsic differences in competitive ability between individuals other than the ones considered and tested for in each model; thereby, winner–loser effects and possible residual effects of dominance ranks not accounted for by our predictors were excluded. CIs were calculated using the modified Wald method[58] for all GLMMs.

Ethical compliance. Our study was approved by the scientific advisory board of the Tanzania Wildlife Research Institute, the Tanzania Commission for Science and Technology, the Ngorongoro Conservation Area Authority and the Internal Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research (permit no. 2002-04-02). All study procedures were performed in compliance with the ethical regulations of these institutions.

Reporting Summary. Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Code availability. The computer code is available in the R package *vullioud2018* on GitHub (https://github.com/hyenaproject/vullioud2018).

Data availability

The data that support the findings of this study are included in the R package *vullioud2018* available on GitHub (https://github.com/hyenaproject/vullioud2018).

Received: 9 June 2018; Accepted: 11 October 2018;

References

1. Alonzo, S. H. Social and coevolutionary feedbacks between mating and parental investment. *Trends Ecol. Evol.* **25**, 99–108 (2010).
2. Clutton-Brock, T. H. & Huchard, E. Social competition and selection in males and females. *Phil. Trans. R. Soc. B* **368**, 20130074 (2013).
3. Ah-King, M. & Ahnesjö, I. The 'sex role' concept: an overview and evaluation. *Evol. Biol.* **40**, 461–470 (2013).
4. Darwin, C. *The Descent of Man, and Selection in Relation to Sex* (Murray, London, 1871).
5. Andersson, M. B. *Sexual Selection* (Princeton Univ. Press, Princeton, 1994).
6. Clutton-Brock, T. H. *Mammal Societies* (John Wiley, Chichester, 2016).
7. von Engelhardt, N., Kappeler, P. M. & Heistermann, M. Androgen levels and female social dominance in *Lemur catta*. *Proc. R. Soc. B* **267**, 1533–1539 (2000).
8. Hemelrijk, C. K., Wantia, J. & Isler, K. Female dominance over males in primates: self-organisation and sexual dimorphism. *PLoS ONE* **3**, e2678 (2008).
9. Surbeck, M. & Hohmann, G. Intersexual dominance relationships and the influence of leverage on the outcome of conflicts in wild bonobos (*Pan paniscus*). *Behav. Ecol. Sociobiol.* **67**, 1767–1780 (2013).
10. Chase, I. D., Tovey, C., Spangler-Martin, D. & Manfredonia, M. Individual differences versus social dynamics in the formation of animal dominance hierarchies. *Proc. Natl Acad. Sci. USA* **99**, 5744–5749 (2002).
11. Stroebe, K., Nijstad, B. A. & Hemelrijk, C. K. Female dominance in human groups: effects of sex ratio and conflict level. *Soc. Psychol. Personal. Sci.* **8**, 209–218 (2017).
12. Markham, C., Lonsdorf, E. V., Pusey, A. E. & Murray, C. M. Maternal rank influences the outcome of aggressive interactions between immature chimpanzees. *Anim. Behav.* **100**, 192–198 (2015).
13. Bissonnette, A. et al. Coalitions in theory and reality: a review of pertinent variables and processes. *Behaviour* **152**, 1–56 (2015).
14. Weiß, B. M. & Kotrschal, K. Effects of passive social support in juvenile greylag geese (*Anser anser*): a study from fledging to adulthood. *Ethology* **110**, 429–444 (2004).
15. Frank, L. G. Social organization of the spotted hyaena *Crocuta crocuta*. II. Dominance and reproduction. *Anim. Behav.* **151**, 1510–1527 (1986).
16. Watts, H. E., Tanner, J. B., Lundrigan, B. L. & Holekamp, K. E. Post-weaning maternal effects and the evolution of female dominance in the spotted hyena. *Proc. R. Soc. B* **276**, 2291–2298 (2009).
17. Gould, S. J. Hyena myths and realities. *Nat. Hist.* **90**, 16–24 (1981).
18. Swanson, E. M. et al. Ontogeny of sexual size dimorphism in the spotted hyena (*Crocuta crocuta*). *J. Mammal.* **94**, 1298–1310 (2013).
19. Smale, L., Frank, L. G. & Holekamp, K. E. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with adult females and immigrant males. *Anim. Behav.* **46**, 467–477 (1993).
20. Höner, O. P. et al. Female mate-choice drives the evolution of male-biased dispersal in a social mammal. *Nature* **448**, 798–801 (2007).
21. Davidian, E., Courtiol, A., Wachter, B., Hofer, H. & Höner, O. P. Why do some males choose to breed at home when most other males disperse?. *Sci. Adv.* **2**, e1501236 (2016).
22. Smith, J. E. et al. Evolutionary forces favoring intragroup coalitions among spotted hyenas and other animals. *Behav. Ecol.* **21**, 284–303 (2010).
23. East, M. L., Hofer, H. & Wickler, W. The erect 'penis' is a flag of submission in a female-dominated society: greetings in Serengeti spotted hyenas. *Behav. Ecol. Sociobiol.* **33**, 355–370 (1993).
24. Clobert, J., Le Galliard, J.-F., Cote, J., Meylan, S. & Massot, M. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12**, 197–209 (2009).
25. Bissonnette, A., de Vries, H. & van Schaik, C. P. Coalitions in male Barbary macaques, *Macaca sylvanus*: strength, success and rules of thumb. *Anim. Behav.* **78**, 329–335 (2009).
26. Sánchez-Tójar, A., Schroeder, J. & Farine, D. R. A practical guide for inferring reliable dominance hierarchies and estimating their uncertainty. *J. Anim. Ecol.* **87**, 594–608 (2018).
27. Hofer, H. & East, M. L. Behavioral processes and costs of co-existence in female spotted hyenas: a life history perspective. *Evol. Ecol.* **17**, 315–331 (2003).

28. MacLeod, K. J. & Lukas, D. Revisiting non-offspring nursing: allonursing evolves when the costs are low. *Biol. Lett.* **10**, 20140378 (2014).
29. Digby, L. in *Infanticide by Males and its Implications* (eds van Schaik, C. P. & Janson, C. H.) 423–446 (Cambridge Univ. Press, Cambridge, 2000).
30. Hofer, H. & East, M. L. in *Serengeti II: Dynamics, Management, and Conservation of an Ecosystem* (eds Sinclair, A. R. E. & Arcese, P.) 332–363 (Univ. Chicago Press, Chicago, 1995).
31. East, M. L. et al. Maternal effects on offspring social status in spotted hyenas. *Behav. Ecol.* **20**, 478–483 (2009).
32. Lukas, D. & Huchard, E. The evolution of infanticide by females in mammals. Preprint at https://www.biorxiv.org/content/early/2018/09/03/405688 (2018).
33. Gowaty, P. A. & Hubbell, S. P. Reproductive decisions under ecological constraints: it's about time. *Proc. Natl Acad. Sci. USA* **106**, 10017–10024 (2009).
34. Lehtonen, J., Parker, G. A. & Schärer, L. Why anisogamy drives ancestral sex roles. *Evolution* **70**, 1129–1135 (2016).
35. Kappeler, P. M. Sex roles and adult sex ratios: insights from mammalian biology and consequences for primate behaviour. *Phil. Trans. R. Soc. B* **372**, 20160321 (2017).
36. Holekamp, K. E. & Smale, L. Dominance acquisition during mammalian social development: the 'inheritance' of maternal rank. *Am. Zool.* **31**, 306–317 (1991).
37. Mills, M. G. L. *Kalahari Hyenas: Comparative Behavioral Ecology of Two Species* (Chapman & Hall, London, 1994).
38. East, M. L. & Hofer, H. Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females. *Behav. Ecol.* **12**, 558–568 (2001).
39. Kruuk, H. *The Spotted Hyena: A Study of Predation and Social Behavior* (Univ. Chicago Press, Chicago, 1972).
40. Hofer, H. & East, M. L. The commuting system of Serengeti spotted hyaenas: how a predator copes with migratory prey. II. Intrusion pressure and commuters' space use. *Anim. Behav.* **46**, 559–574 (1993).
41. Höner, O. P. et al. The fitness of dispersing spotted hyaena sons is influenced by maternal social status. *Nat. Commun.* **1**, 60 (2010).
42. East, M. L. & Hofer, H. Loud-calling in a female-dominated mammalian society: II. Behavioural contexts and functions of whooping of spotted hyaenas, *Crocuta crocuta*. *Anim. Behav.* **42**, 651–669 (1991).
43. Holekamp, K. E. & Smale, L. Ontogeny of dominance in free-living spotted hyaenas: juvenile rank relations with other immature individuals. *Anim. Behav.* **46**, 451–466 (1993).
44. Benhaiem, S., Hofer, H., Kramer-Schadt, S., Brunner, E. & East, M. L. Sibling rivalry: training effects, emergence of dominance and incomplete control. *Proc. R. Soc. B* **279**, 3727–3735 (2012).
45. Frank, L. G., Glickman, S. E. & Licht, P. Fatal sibling aggression, precocial development, and androgens in neonatal spotted hyenas. *Science* **252**, 702–704 (1991).
46. Smale, L., Holekamp, K. E., Weldele, M., Frank, L. G. & Glickman, S. E. Competition and cooperation between litter-mates in the spotted hyaena, *Crocuta crocuta*. *Anim. Behav.* **50**, 671–682 (1995).
47. Wilhelm, K. et al. Characterization of spotted hyena, *Crocuta crocuta* microsatellite loci. *Mol. Ecol. Notes* **3**, 360–362 (2003).
48. Kalinowski, S. T., Taper, M. L. & Marshall, T. C. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. *Mol. Ecol.* **16**, 1099–1106 (2007).
49. Trinkel, M., Fleischmann, P. H. & Kastberger, G. Comparison of land-use strategies of spotted hyenas (*Crocuta crocuta*, Erxleben) in different ecosystems. *Afr. J. Ecol.* **44**, 537–539 (2006).
50. Kolowski, J. M. & Holekamp, K. E. Ecological and anthropogenic influences on space use by spotted hyaenas. *J. Zool.* **277**, 23–36 (2009).
51. Ilany, A. & Akçay, E. Social inheritance can explain the structure of animal social networks. *Nat. Commun.* **7**, 12084 (2016).
52. Wachter, B., Höner, O. P., East, M. L., Golla, W. & Hofer, H. Low aggression levels and unbiased sex ratios in a prey-rich environment: no evidence of siblicide in Ngorongoro spotted hyenas (*Crocuta crocuta*). *Behav. Ecol. Sociobiol.* **52**, 348–356 (2002).
53. Wood, S. N. *Generalized Additive Models: An Introduction with R* (CRC Press, Boca Raton, 2017).
54. Frank, L. G., Glickman, S. E. & Powch, I. Sexual dimorphism in the spotted hyaena (*Crocuta crocuta*). *J. Zool.* **221**, 308–313 (1990).
55. R Development Core Team *R: A Language and Environment for Statistical Computing* (R Foundation for Statistical Computing, Vienna, 2018).
56. Rousset, F. & Ferdy, J.-B. Testing environmental and genetic effects in the presence of spatial autocorrelation. *Ecography* **37**, 781–790 (2014).
57. Breslow, N. E. & Clayton, D. G. Approximate inference in generalized linear mixed models. *J. Am. Stat. Assoc.* **88**, 9–25 (1993).
58. Agresti, A. & Coull, B. A. Approximate is better than 'exact' for interval estimation of binomial proportions. *Am. Stat.* **52**, 119–126 (1998).
59. Wolff, J. O. & MacDonald, D. W. Promiscuous females protect their offspring. *Trends Ecol. Evol.* **19**, 127–134 (2004).

Acknowledgements

We thank the Tanzania Commission for Science and Technology for permission to conduct the study, the Tanzania Wildlife Research Institute, Ngorongoro Conservation Area Authority, D. Thierer, S. Karl, M. Szameitat and P. Naman for their assistance and E. Huchard, M. Franz, O. Judson and P. Vullioud for helpful comments. The study was financed by the Leibniz Institute for Zoo and Wildlife Research, the Werner Dessauer Stiftung, the Stiftung Naturschutz and private donors.

Author contributions

Conceptualization: O.P.H., A.C. and E.D. Methodology: A.C., C.V., F.R. and O.P.H. Software: C.V., A.C. and F.R. Formal analysis: C.V., A.C. and F.R. Investigation: O.P.H., E.D. and B.W. Resources: O.P.H. Data curation: O.P.H., C.V. and A.C. Writing of original draft: O.P.H., E.D., A.C. and C.V. Review and editing of draft: O.P.H., E.D, A.C., C.V., B.W. and F.R. Supervision: O.P.H. and A.C. Project administration: O.P.H. Funding acquisition: O.P.H.

Competing interests

The authors declare no competing interests.

Additional information

Supplementary information is available for this paper at https://doi.org/10.1038/s41559-018-0718-9.

Reprints and permissions information is available at www.nature.com/reprints.

Correspondence and requests for materials should be addressed to O.P.H.

natureresearch

Corresponding author(s): Oliver P. Höner

Reporting Summary

Nature Research wishes to improve the reproducibility of the work that we publish. This form provides structure for consistency and transparency in reporting. For further information on Nature Research policies, see Authors & Referees and the Editorial Policy Checklist.

Statistical parameters

When statistical analyses are reported, confirm that the following items are present in the relevant location (e.g. figure legend, table legend, main text, or Methods section).

n/a	Confirmed	
☐	☒	The exact sample size (*n*) for each experimental group/condition, given as a discrete number and unit of measurement
☐	☒	An indication of whether measurements were taken from distinct samples or whether the same sample was measured repeatedly
☐	☒	The statistical test(s) used AND whether they are one- or two-sided *Only common tests should be described solely by name; describe more complex techniques in the Methods section.*
☐	☒	A description of all covariates tested
☐	☒	A description of any assumptions or corrections, such as tests of normality and adjustment for multiple comparisons
☐	☒	A full description of the statistics including central tendency (e.g. means) or other basic estimates (e.g. regression coefficient) AND variation (e.g. standard deviation) or associated estimates of uncertainty (e.g. confidence intervals)
☐	☒	For null hypothesis testing, the test statistic (e.g. *F*, *t*, *r*) with confidence intervals, effect sizes, degrees of freedom and *P* value noted *Give P values as exact values whenever suitable.*
☒	☐	For Bayesian analysis, information on the choice of priors and Markov chain Monte Carlo settings
☐	☒	For hierarchical and complex designs, identification of the appropriate level for tests and full reporting of outcomes
☐	☒	Estimates of effect sizes (e.g. Cohen's *d*, Pearson's *r*), indicating how they were calculated
☐	☒	Clearly defined error bars *State explicitly what error bars represent (e.g. SD, SE, CI)*

Our web collection on statistics for biologists may be useful.

Software and code

Policy information about availability of computer code

Data collection	No software was used to collect the behavioural data.
Data analysis	Parentage analyses were done using CERVUS 3.0.3. All other analyses were done using custom code for R version 3.5.1.

For manuscripts utilizing custom algorithms or software that are central to the research but not yet described in published literature, software must be made available to editors/reviewers upon request. We strongly encourage code deposition in a community repository (e.g. GitHub). See the Nature Research guidelines for submitting code & software for further information.

Data

Policy information about availability of data

All manuscripts must include a data availability statement. This statement should provide the following information, where applicable:

- Accession codes, unique identifiers, or web links for publicly available datasets
- A list of figures that have associated raw data
- A description of any restrictions on data availability

The data sets and computer code used for this study are included in the R package vullioud2018 freely available on GitHub (https://github.com/hyenaproject/vullioud2018)

Field-specific reporting

Please select the best fit for your research. If you are not sure, read the appropriate sections before making your selection.

☐ Life sciences ☐ Behavioural & social sciences ☒ Ecological, evolutionary & environmental sciences

For a reference copy of the document with all sections, see nature.com/authors/policies/ReportingSummary-flat.pdf

Ecological, evolutionary & environmental sciences study design

All studies must disclose on these points even when the disclosure is negative.

Study description	We observed dyadic interactions between spotted hyaenas of the same and different sex in different social contexts (intraclan and interclan). We used generalised linear mixed-effects models to predict the outcome of the interactions based on the difference between the two interacting individuals in their potential social support, body mass, immigration status and sex.
Research sample	We observed interactions between all individually known spotted hyaenas older than one year of age of all eight clans inhabiting the Ngorongoro Crater, Tanzania, between April 1996 and December 2017. We collected behavioural, morphological, life history and genetic pedigree data from eight different clans to obtain behavioural data from various social contexts and disentangle the effects of intrinsic attributes and social support. Analyses were based on 4133 dyadic interactions between 748 spotted hyaenas.
Sampling strategy	Observations of dyadic interactions were collected ad libitum and during focal follows. Sample sizes were sufficient as seen by the low confidence intervals of the predicted winning probabilities and growth curves, and the exceptionally high exclusionary power (0.999) and assignment success rate at the 95% confidence level (97.2%) of parentage assignments.
Data collection	Behavioural observations and samples for parentage analysis were collected by three authors (E.D., B.W., O.P.H.) ad libitum and during focal follows. Behavioural observations were done from a research vehicle stationed at some distance from the study animals; all study animals were well habituated to the presence of the research vehicle. Samples for parentage analysis were collected using non-invasive methods.
Timing and spatial scale	Data were collected during continuous monitoring of the entire population in the Ngorongoro Crater between April 1996 and December 2017 to obtain sufficiently large sample sizes.
Data exclusions	The types of observations excluded in the analysis, the justification for the exclusion and the sample sizes of excluded data are described in the methods section. The exclusion of data was established before fitting the models.
Reproducibility	No experiments were performed in this study. The outcome of interactions was established based on conspicuous behaviours and body postures that clearly indicate dominance and submission. These behaviours and body postures were predefined and have been applied for decades by all scientists studying spotted hyaenas.
Randomization	Study animals were not allocated into groups but categorised based on intrinsic attributes (sex, body mass, age), location, immigration status, and their potential social support as estimated by an algorithm based on decision rules derived from previously established patterns of social support and a detailed genetic pedigree spanning 21 years and eight generations. Following traditional multiple linear regression framework, the effects of the covariates were estimated while statistically controlling for the effects of the others. We additionally used natural experiments to disentangle causality between the covariates.
Blinding	Study animals were identified before interactions were recorded. Behaviours and interactions were categorised and analysed following a standardised protocol and ethogram.

Did the study involve field work? ☒ Yes ☐ No

Field work, collection and transport

Field conditions	Mean daily temperature: 13°C to 16°C. Precipitation: approximately 1000mm per year.
Location	Ngorongoro Crater, Tanzania, latitude: 3.16°S, longitude: 35.59°E, altitude: 1800mamsl
Access and import/export	Collection of samples for parentage analysis: Research Permit No. 2018-321-NA-90-130, issued by Tanzania Commission for Science and Technology, Dar es Salaam, Tanzania Export of samples: Trophy Export Certificate No. 72763, issued by Tanzania Wildlife Authority, Dodoma, Tanzania Export of samples: Animal Health Export Certificate No. VIC/AR/ZIS/2308, issued by Ministry of Livestock & Fisheries of Tanzania, Arusha, Tanzania Import of samples: no permit required as per directive by the Senate Department for Justice, Consumer Protection and Anti-Discrimination (Senatsverwaltung für Justiz, Verbraucherschutz und Antidiskriminierung), Berlin, Germany
Disturbance	Observations were made from a research vehicle stationed at some distance from the study animals; all study animals were well habituated to the presence of the research vehicle.

Reporting for specific materials, systems and methods

Materials & experimental systems

n/a	Involved in the study	
☒	☐	Unique biological materials
☒	☐	Antibodies
☒	☐	Eukaryotic cell lines
☒	☐	Palaeontology
☐	☒	Animals and other organisms
☒	☐	Human research participants

Methods

n/a	Involved in the study	
☒	☐	ChIP-seq
☒	☐	Flow cytometry
☒	☐	MRI-based neuroimaging

Animals and other organisms

Policy information about studies involving animals; ARRIVE guidelines recommended for reporting animal research

Laboratory animals	The study did not involve laboratory animals.
Wild animals	Spotted hyaenas (Crocuta crocuta) in the Ngorongoro Crater, Tanzania. Animals were observed from distance from a research vehicle to which the animals were well habituated; samples were collected without capturing or immobilising animals.
Field-collected samples	Samples for parentage analysis were stored in liquid nitrogen or DMSO; samples stored in liquid nitrogen were transported on dry ice from the field in Tanzania to the laboratory in Berlin and kept at -80°C until processing.