



Aggressiveness and submissiveness in spotted hyaenas: one trait or two?

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Aggressive and submissive behaviours are commonly assumed to represent two extremes of a single personality trait, often labelled 'aggressiveness'. However, most studies focus exclusively on submissive behaviour elicited by conspecific aggression, and on rates at which aggressive and submissive behaviours are expressed, without considering either unprovoked submissive behaviour, or the intensity of the actions themselves. Utilizing a long-term data set spanning 27 years of dyadic agonistic interactions among spotted hyaenas, *Crocuta crocuta*, including counts and intensities of all unprovoked acts of aggressive and submissive behaviour, we assessed consistency within individuals in these behaviours. We found that counts of acts of both aggression and submission performed by adult female hyaenas varied with context, that neither measure was consistent within individuals over time and that both were strongly affected by social rank, suggesting that neither of these rate measures represent personality traits. Although rank influenced the intensity of submissive acts, intensity of aggressive acts did not vary with rank. Intensities of aggressive and submissive acts also varied with context, but both were consistent within individual females regardless of age, suggesting that both intensity measures may represent personality traits. We found no significant correlation between individual lifetime averages of intensities of aggressive and submissive behaviour, supporting the hypothesis that these may represent different traits rather than opposite ends of a single spectrum. Lifetime rates at which females performed acts of aggression and submission were uncorrelated with fitness, but analysis of the average intensity of aggressive or submissive acts performed by adult female hyaenas suggests that lifetime reproductive success may be lower at both ends of the spectrum of behavioural intensity than in its centre after controlling for rank, suggesting the action of stabilizing selection.

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In animal societies structured by linear dominance hierarchies, outcomes of dyadic agonistic interactions are usually determined by the subordinate's behaviour in response to an aggressive act, and the aggressor is considered to 'win' the altercation if it receives a submissive response (de Vries, 1998; de Vries et al., 2006; Gammel et al., 2003). This means that more dominant individuals win more aggressive altercations, and less dominant individuals submit more often. Therefore, some have suggested that a subordination hierarchy might be a more useful concept than a dominance hierarchy (e.g. Rowell, 1974). Furthermore, many highly cited articles on agonistic behaviour (e.g. Bernstein, 1981; Drews, 1993; Lewin et al., 1939; Sapolsky, 2004; Tiedens & Fragale, 2003) can be interpreted to suggest that aggressive and submissive behaviours represent

two ends of a single continuum (Fig. 1a) based on the number of agonistic interactions an individual wins or loses in a dominance relationship. However, this common assumption of a negative correlation between aggressive and submissive behaviour spectra usually only considers submissive behaviour that occurs in response to conspecific aggression. Here instead we focus exclusively on unprovoked submissive behaviour, which is spontaneous appeasement behaviour not expressed in response to a preceding aggressive act directed at the actor by a groupmate.

An alternative hypothesis (Fig. 1b) suggests that aggressiveness and submissiveness may represent two independent personality dimensions, such that individuals vary consistently in these traits in different ways, and that the traits may even have different effects on fitness. Here we suggest that the study of unprovoked acts of aggression and submission can shed light on whether aggressiveness and submissiveness represent one personality dimension or two. As emphasized by Nelson and Kriegsfeld (2017), this is not a

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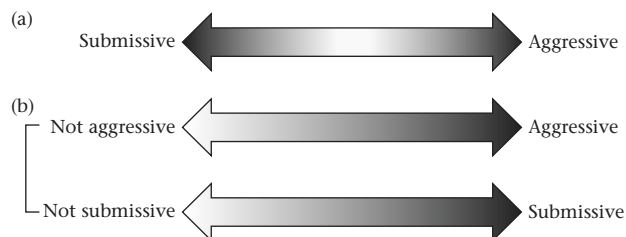


Figure 1. Two models of agonistic behaviour: aggressive and submissive behaviours can be conceptualized either (a) as opposite ends of a single behavioural continuum or (b) as two separate aspects of an individual's behaviour (modified from Nelson & Kriegsfeld, 2017).

trivial semantic issue, but rather an important conceptual one, because our assumptions about whether aggression and submission represent one behavioural dimension or two influence the way both the proximal mediation of agonistic behaviour and its survival value are assessed (Schlinger & Callard, 1990). For example, the hormonal mediation of the aggressive and submissive components of an agonistic interaction may differ (Leshner & Moyer, 1975). In fact, the hypothesis that aggression and submission represent independent personality dimensions is supported by research on the neural and genetic correlates of aggressive behaviour in humans and laboratory animals, suggesting underlying mechanisms that may be shared across mammalian taxa (de Almeida et al., 2005; Ferrari et al., 2005; Kiser et al., 2012; Lischinsky & Lin, 2020); this work suggests that aggressiveness and submissiveness may either be uncorrelated, or even positively correlated if both indicate general reactivity to social stimuli. However, we know very little about whether aggression and submission represent one dimension or two in free-living nonhuman mammals, perhaps in part because addressing such questions demands access to detailed long-term data sets that quantify both rates and intensities of agonistic acts.

Quantification of personality traits in highly social free-living mammals typically requires intensive long-term study to record behavioural data, such that repeated measures of a specific trait can be obtained from each individual to assess its consistency within individuals. Animal personality traits are characterized by consistency within individuals over time and among contexts (e.g. Sih & Bell, 2007). Here we use detailed, longitudinal data documenting rates and intensities of unprovoked aggressive and submissive behaviours in a wild population of spotted hyaenas, *Crocuta crocuta*, that we have followed for many years in Kenya. In contrast to many other field studies of free-living mammals, we record not only the number of unprovoked acts of aggression and submission observed, but also the intensity of these behaviours. By focusing on unprovoked behaviours, we hope to assay the consistency of the individual's unprovoked behaviour, rather than its reactive behaviour, which may be controlled by a different set of underlying mechanisms.

The spotted hyaena is unique among mammalian carnivores in that its social structure resembles that of many cercopithecine primates (Holekamp, 2017). However, in contrast to cercopithecine primates, adult female hyaenas dominate all immigrant males (Kruuk, 1972), who sire most cubs in hyaena societies (Engh et al., 2002; Van Horn et al., 2004). Much like cercopithecine primate groups, spotted hyaena clans are structured by matrilineal, linear dominance hierarchies in which cubs acquire social ranks just below those of their mothers (Engh et al., 2000; Strauss et al., 2020); in fact, cubs acquire the entire social networks of their mothers in a complex process of nongenetic inheritance (Ilany et al., 2021) that is maintained via learning through successive generations (Engh et al., 2000; Strauss et al., 2020). This well-

studied clan structure permits us to analyse unprovoked aggressive and submissive behaviour within the context of a dominance hierarchy and control for each subject's social rank at the time of each observation. This in turn allows us to determine whether unprovoked aggressive and submissive behaviours are individually consistent across time and contexts, as expected of a personality trait, and whether differences in these behaviours are driven primarily by social rank, or whether both rank and individual differences affect their occurrence.

Some personality traits have already been defined and assessed in spotted hyaenas, including boldness, sociability and aggressiveness (Gosling, 1998; Greenberg & Holekamp, 2017; Yoshida et al., 2016). In particular, Yoshida et al. (2016) found that aggressiveness was consistent over time within individual hyaenas, based on the intensity of their aggressive behaviour, but that the rates at which they performed aggressive acts was not. These authors also found that rates, but not intensities, of aggressive acts were positively correlated with fitness in female spotted hyaenas. Specifically, after calculating a lifetime measure of aggressiveness for each individual, they found that the offspring of more aggressive females survived better than did offspring of less aggressive females, after controlling for social rank. However, these analyses were completed with much smaller data sets than we have now, and the authors failed to consider submissive behaviour at all and focused exclusively on actions directed down the hierarchy.

Our primary goal here was to determine whether individuals are consistent with respect to the rates and intensities at which they perform unprovoked aggressive and submissive behaviours. If submissiveness represents a personality dimension distinct from aggressiveness, then observations of social interactions involving unprovoked acts of submissive behaviour should reveal individual consistency through repeated measures across time and across multiple contexts. Our second goal was to test the hypothesis that unprovoked submissiveness represents a different personality trait from unprovoked aggressiveness. Unprovoked submissive acts obviate the need for aggression, because they function to make clear to a potential aggressor that the submitting hyaena recognizes its status as lower than that of the potential aggressor. We tested this hypothesis by determining whether submissiveness and aggressiveness are negatively correlated within individuals, uncorrelated within individuals or positively correlated, as might occur if both reflect overall emotional or social reactivity. Either of these latter findings would oppose the notion that aggressiveness and submissiveness are negatively correlated. Finally, we inquired whether these traits have significant independent effects on offspring survival after controlling for social rank. Although past work indicated that higher rates of aggressive behaviour enhance reproductive success among females (Watts et al., 2009; Yoshida et al., 2016), here we use data collected over nearly three decades to inquire whether either rates or intensities of aggressive and submissive behaviour affect fitness when social rank is included in the same model. If these are truly two separate traits, then the two traits may have different effects on fitness, suggesting an evolutionary mechanism for maintaining individual variation in agonistic behaviour within a social species where rank is known to have large effects on fitness (Hofer & East, 2003; Holekamp et al., 1996). We focus exclusively on dyadic agonistic interactions because fitness effects of coalitionary aggression have been well studied previously (Smith et al., 2008; Strauss & Holekamp, 2020; Vulliamd et al., 2019), and because coalitionary aggression in the fission–fusion societies of spotted hyaenas is so variable that it cannot be used to assess individual consistency in agonistic behaviour. Finally, we focus exclusively on aggressive and submissive behaviours not elicited by a preceding agonistic action; we refer to these as unprovoked behaviours.

METHODS

Observations of Behaviour

Observational data were collected between 1989 and 2016 from one large social group, or 'clan', of hyaenas inhabiting the Talek region of the Masai Mara National Reserve, Kenya. Individuals were identified based on their unique spots and other identifying marks, such as scars and ear damage. The sex of each individual was determined based on the shape of the glans of its erect phallus (Frank et al., 1990), and ages of natal animals were determined based on cub appearance when first seen (Holekamp et al., 1996). Mother–offspring relationships were based on observations of cubs nursing (Holekamp & Smale, 1998) and genotyping through microsatellite profiling (Engh et al., 2000; Van Horn et al., 2004), allowing for a count of the total number of cubs produced during a female's lifetime.

Observations were made daily from vehicles for 3–4 h around dawn and again around dusk. We defined an observation session as finding one or more hyaenas separated from others by at least 200 m, as described previously (Yoshida et al., 2016); observation sessions lasted from 5 min to several hours. However, sessions lasting 5 min were typically those where the observer stopped only to identify hyaenas and then moved on. Therefore, we restricted our analyses to observation sessions lasting 10 min or longer. Additionally, we restricted our data set to include only those observation sessions in which at least two hyaenas were present. During each observation session, we identified all hyaenas present to calculate group size and used all-occurrence sampling (Altmann, 1974) to record all aggressive and submissive acts. We then restricted our analyses to acts that were clearly not occurring in response to a preceding agonistic behaviour directed at the actor by a groupmate. All observation sessions were excluded from our analyses in which observers were unable to conduct complete all-occurrence sampling of agonistic behaviours due to either poor observation conditions or the presence of at least one hyaena we were unable to identify. We also recorded the context in which each agonistic interaction occurred as either with 'food', at a kill or carcass, at a communal 'den', or elsewhere ('other'), where hyaenas were generally travelling or resting together. Sessions at natal dens and where mating occurred were not included due to the rarity of observing individuals in these contexts multiple times during their lives. Because agonistic behaviour might vary with local food availability, we assessed average prey abundance twice each month by counting prey along multiple 4 km transects within the Talek clan's territory (Green et al., 2019). Monthly prey count data were assigned as either high or low, depending on whether they were higher or lower in that month than the average prey availability during that year.

Social ranks were assigned based on wins and losses in dyadic agonistic encounters between individuals within the study clan each year. From this, a dominance matrix could be calculated annually for adults of each sex (Strauss & Holekamp, 2019). Cubs were assigned their mother's rank until they reached reproductive maturity at 24 months of age, at which point females were classified as adults and entered the adult female hierarchy with their own ranks. After male spotted hyaenas reach reproductive maturity they typically disperse to new clans, where they join the hierarchy in the new clan at the lowest possible rank position, below all natal individuals and other immigrant males that arrived earlier, only ascending in rank when males ahead of them in the immigrant queue die or disperse to new clans (East et al., 2003). All ranks were assigned annually. Although rank is fairly stable over long periods within our study clans, births and deaths do lead to small shifts. To help control for this, every newly reproductive female that was

alive at some point in the year for which a rank matrix was calculated was assigned a rank below that of her mother. Ranks were then standardized by dividing numerical ranks by the number of hyaenas present in the clan in that year and then centred from -1 to 1. Finally, given the philopatric nature of female spotted hyaenas and our ability to assess their lifetime reproductive success, the data used in our analyses only include observations of aggressive and submissive acts performed by adult (>24 months) females. This allowed us to count the number of lower-ranking individuals present with the focal hyaena in each observation session in our analyses of aggressive behaviour and to count the number of higher-ranking individuals present with the focal hyaena in our analyses of submissive behaviour.

Counts of Aggressive and Submissive Behaviour

Because we considered only dyadic interactions, we were able to avoid any confounding effects of support from groupmates during agonistic encounters. Counts of aggressive or submissive behaviours expressed during dyadic agonistic interactions within each observation session involved assessing how many times a hyaena either aggressed upon a groupmate or submitted to a groupmate, respectively, during an observation session without any immediately preceding agonistic action from any groupmate. To ensure we were recording only unprovoked behaviour, we removed cases in which any agonistic behaviour involving the actor occurred during the preceding minute of observation. The groupmate to which aggressive or submissive behaviour was directed was identified based on its proximity, the actor's body orientation and the actor's viewing direction. However, all acts were excluded from our data set for which an actor directed its unprovoked behaviour at multiple groupmates concurrently, or if for any other reason we could not identify the intended recipient of the behavioural act.

We considered all unprovoked aggressive and submissive acts regardless of whether they were directed up or down the hierarchy. From counts within observation sessions, hourly rates could be calculated and corrected for both observation time and number of groupmates present with the focal hyaena. Thus, we calculated an hourly rate of behaviour, controlled for opportunity to perform that behaviour, for each adult female in each observation session as follows: (number of actions performed/number of groupmates present/(observation session length in minutes/60)).

Intensities of Aggressive and Submissive Behaviour

We recorded the intensity of both aggressive and submissive acts on separate three-point scales, with 3 being the most intense. The aggressive behaviours we recorded included (1) intention movements to attack, such as head waves, (2) threat and attack behaviours without bodily contact, such as lunges, jaw snapping and chases and (3) physical contact that might result in injury, such as biting and tackling. Similar intensity categories for unprovoked submissive behaviours were also assigned, from lowest to highest as (1) minor appeasement signals, such as flattening the ears back against the head or headbobbing, (2) postural changes such as folding the entire body into a submissive posture with tail down between the legs and (3) 'groveling', or crawling on one's belly and carpal (Kruuk, 1972). Descriptions of these behaviours can be found in the Appendix. Vocal signals were not included as acts of aggression or submission because the meanings of most hyaena vocalizations have yet to be determined and some vocalizations have been observed to occur in several different social contexts (e.g. East & Hofer, 1991; Theis et al., 2007).

Correlation between Aggression and Submission within Individuals

If we found that an agonistic measure was consistent across time or context within individuals, we referred to it as a personality 'trait', then compared consistent submissive and aggressive traits within a single model. That is, we assessed the correlation between measures (either counts or intensities) of aggressive and submissive acts within individuals. Hourly rates of behaviour within observation sessions were aggregated for each female to calculate her mean lifetime rate of performing aggressive or submissive behaviour, starting when she reached 24 months of age; then we normalized the data by taking the square root of each rate calculation. To calculate mean lifetime intensities of aggressive and submissive acts performed by each female, we aggregated the intensity scores for all her acts of aggression or submission, which were normally distributed. We also utilized these mean lifetime rates and intensities of aggressive and submissive behaviour in our assessment of effects on fitness.

Assessment of Fitness

Each female's lifetime reproductive success was calculated by counting her offspring that survived at least to 24 months, which is the age at which spotted hyaenas are physiologically competent to breed (Glickman et al., 1992). These numbers were then divided by the mother's age at death in years to calculate an annual lifetime rate at which her offspring survived to sexual maturity, and to normalize the data we calculated the square root of each value. Here we focused only on females in our data set for which we knew both their birth and death dates, allowing for analyses of 72 females.

For any behavioural measure that was consistent over time within females, we considered lifetime reproductive success in relation to each female's lifetime mean value of that behavioural measure. We used the mean lifetime values of aggressive and submissive acts calculated for each adult female as described above, from all sessions in which she was observed starting when she was 24 months old. By calculating rates of behaviour corrected for the number of other hyaenas present, we were also able to assess effects on lifetime reproductive success of aggressiveness or submissiveness with social rank as a separate predictor; rank is well known to have large effects on fitness in female spotted

hyaenas (Holekamp et al., 1996; Swanson et al., 2011; Turner et al., 2020). To account for slight changes in rank across a female's lifetime, we calculated a mean lifetime rank for each female as her mean rank across all observation sessions in which she was present in the clan as an adult. These mean lifetime ranks, and lifetime mean rates and intensities of aggressive and submissive behaviour, were included as factors in each fitness model to distinguish their effects on offspring survival from those of social rank alone.

Data Analysis

Given our interest in individual differences, we chose to utilize a mixed model approach for quantifying individual variation, allowing us to treat individual identity as a random factor in our models, and compare the fit of models with and without this random factor included (Dingemans & Dochtermann, 2013). For both number of acts (counts) and intensities of agonistic behaviours, we built models for analysing the individual level fixed effect of standardized social rank (Tables 1, 2). We also included relevant session level fixed effects as predictors in the model, including the total number of hyaenas present, the context of the session (food, den or other), prey density (high or low) in the month when the observation occurred to account for variation in motivation to interact over food resources and the proportion of hyaenas present in each observation session that were either lower-ranking than the actor for aggressive behaviour or higher-ranking than the actor for submissive behaviour. Age was also included in these models to determine whether a female's agonistic behaviour was consistent over time after the onset of adulthood. For each female this included all observations between 24 months of age and her death. The median age at time of death for females surviving to 24 months in our sample was ~7 years of age.

Analyses of all models were conducted in R v.4.0.0 and R Studio Desktop v.1.2.5042. Collinearity diagnostics for fixed model predictors were done during model selection using the R package 'olsrr' (Hebbali, 2020), ensuring that variance inflation factors did not exceed 4 and that condition indices between variables were within acceptable limits to avoid collinearity among fixed factors. All social factors (rank, proportion of targets, group size) were tested for interaction effects, and if these were found to be significant, they were included in the final model (Tables 1, 2).

Table 1
MCMCglmm model description for biological and random factors predicting the number of times female hyaenas perform unprovoked acts of aggression or submission in observation sessions, with definitions of fixed and random effects

| Variable of interest | Fixed effects | Definition | Random effects | Interaction effect |
|--|------------------------------|---|--|---------------------------------|
| Count of behaviour (sum of aggressive or submissive acts within each session, with a zero-inflated Poisson distribution) | Duration | Number of minutes within an observation session | Session (observation session number as a factor) | Group size X proportion targets |
| | Context (den, food or other) | Food (a kill or carcass present), den (an active hyaena den present), other (all other sessions) | ID (identity of the individual hyaena) | |
| | Standardized rank | Rank of the individual in the hierarchy controlled for number of ranked individuals in the clan | | |
| | Age | Age of the individual on the date of the session | | |
| | Group size | Number of hyaenas present during an observation session | | |
| | Proportion targets | Ratio of number of ranked individuals (in relation to the acting hyaena) divided by the group size in a session | | |
| | Prey density (high or low) | Monthly average vs annual average of prey transect counts | | |

Table 2

MCMCglmm model for predicting the intensity of unprovoked acts of aggressive or submissive behaviour performed by female hyaenas, with definitions of fixed and random effects

| Variable of interest | Fixed effects | Definition | Random effects | Interaction effects |
|--|------------------------------|---|--|---------------------|
| Intensity of behaviour (ordinal scale 1, 2 or 3, with 1 being lowest and 3 being highest, for aggressive or submissive acts) | Context (den, food or other) | Food (a kill or carcass present), den (an active hyaena den present), other (all other sessions) | Session (observation session number as a factor) | None observed |
| | Standardized rank | Rank of the individual in the hierarchy controlled for number of ranked individuals in the clan | ID (identity of the individual hyaena) | |
| | Age | Age of the individual on the date of the session | | |
| | Group size | Number of hyaenas present during an observation session | | |
| | Proportion targets | Ratio of number of ranked individuals (in relation to the acting hyaena) divided by the group size in a session | | |
| | Prey density (high or low) | Monthly average vs annual average of prey transect counts | | |

For final analyses of count and intensity data, we utilized the 'MCMCglmm' package in R (R Core Team, 2020; also see Hadfield, 2010). This Bayesian approach allowed for visual inspection of trace plots to determine whether each model converged to make a good approximation of the posterior distribution for each fixed factor. Fixed effects were tested for significance based on the distribution of their 95% credible intervals, and a pMCMC value indicated whether or not a result was statistically significant. A model factor was only considered significant if its credible interval failed to overlap zero and its pMCMC was less than 0.05. We also tested the significance of a random effect of hyaena identity (ID) by looking at the difference in deviance information criterion values (Δ DIC) between models fitted with and without individual ID included as a random effect. The ID was considered significant, indicating individual consistency, if Δ DIC was -10 or more (Burnham & Anderson, 2002; Hadfield, 2010). Because our counts of acts were calculated even for observation sessions in which focal individuals did not interact with any groupmates present, we utilized zero-inflated Poisson distribution within our MCMCglmm count models. Within these models, length of each observation session was included as a predictor to control for the amount of time the focal individual had in which to act. MCMCglmm models of behavioural intensity were analysed using the family = 'ordinal' specification given that the categorical levels of our defined intensities (1–3) had a natural order (Hadfield, 2010).

Following this, to determine whether rates or intensities of aggressive and submissive behaviour were correlated within individuals, we used the R base linear model package 'lm' to compare lifetime mean values within individuals of each behavioural measure (counts of aggressive and submissive acts or intensities of those acts) if deemed a potential personality trait. We did this using the aggression measure as the dependent variable and the submission measure as the independent variable for each comparison (R Core Team, 2020).

Finally, we used the R package 'lm' to assess reproductive success of each female in relation to her mean lifetime value of each behavioural measure, along with the female's mean lifetime social rank. If the correlation between the behavioural trait and reproductive success was found to be significant when mean rank was included in the model, we plotted the lifetime reproductive success of the female against her lifetime mean for that behavioural measure, as calculated from all observation sessions involving that focal female during her adulthood. We then fitted a best-fit line to the distribution, considering three polynomial relationships (linear,

quadratic, logarithmic) in an initial analysis. The best fit was kept and results were plotted using ggplot2 (Wickham et al., 2016).

RESULTS

Aggressive Behaviour

For models predicting counts of unprovoked aggressive acts, we used 43 157 observation sessions involving 128 adult females who had an opportunity to aggress upon at least one groupmate during each session. The mean length of all observation sessions used here was 46.4 min, with an SEM of 0.16. This data set included sessions in which the female had the opportunity to act because a groupmate was present with her, but failed to do so, leading to a count of zero aggressive acts by that female in that observation session. Within this data set we recorded 10 732 aggressive acts, with 15% directed up the hierarchy and 85% directed downward. The mean number of opportunities to attack when at least one groupmate was present per female was 332 over her lifetime, with a range of 20–1740.

Counts of aggressive acts by adult females

Count of aggressive acts in observation sessions, when controlled for session length, showed some level of consistency within individuals, as the random factor of ID improved model fit (Δ DIC = -47). However, it also appeared that the number of times a female directs aggressive acts towards groupmates was driven largely by rank, contextual factors, age and group size (Fig. 2). First, social rank significantly affected counts of aggressive acts/h (pMCMC = 0.002; Fig. 2b). Second, counts of aggressive behaviour were higher in the presence of food than in other contexts (pMCMC < 0.001; Fig. 2a). Third, we observed a significant interaction between the proportion of targets present who were of lower rank than the actor and overall group size in affecting the likelihood of females performing aggressive acts (pMCMC < 0.001); females performed aggressive acts more often as the proportion of lower-ranking groupmates increased, but how often they performed aggressive acts declined as group size increased (Fig. 2c). Fourth, age was a significant predictor of counts of aggressive acts (pMCMC = 0.034), suggesting variation over time (Fig. 2d), although the effect size was small and is difficult to see in Fig. 2a. Finally, prey density was not correlated with the number of times an individual performed aggressive acts during an observation session (pMCMC = 0.97).

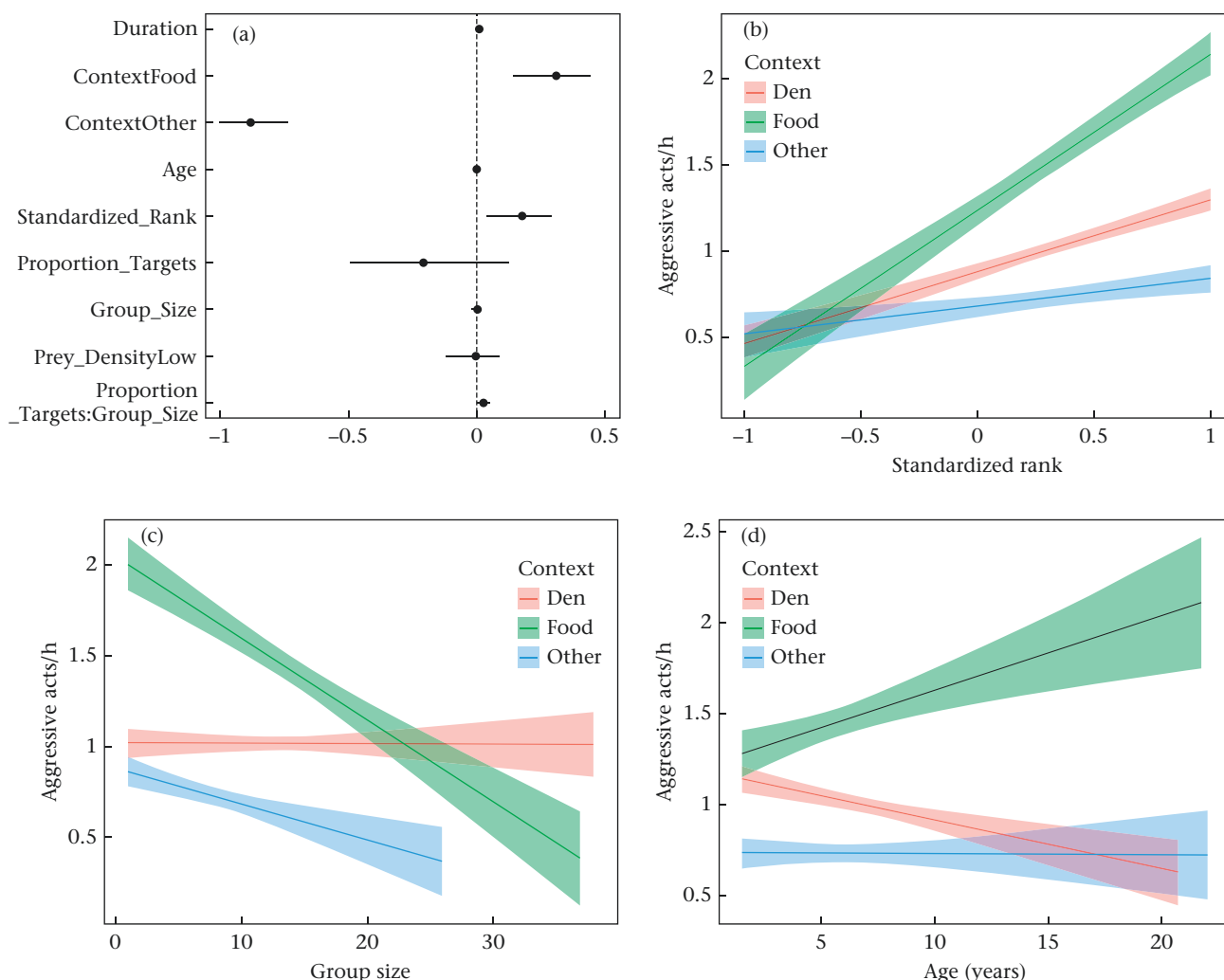


Figure 2. (a) Model assessing fixed predictors of the number of aggressive acts performed by adult females. (b) Aggressive acts performed by adult females/h (count/duration) in different contexts based on their standardized rank in the observation session. The shaded areas surrounding the lines represent 95% confidence intervals. (c) Aggressive acts performed by adult females/h (count/duration) in different contexts based on the group size present in the observation session. The shaded areas surrounding the lines represent 95% confidence intervals. (d) Aggressive acts performed by adult females/h (count/duration) in different contexts based on the age in years of the individual in each observation session where it was present. The shaded areas surrounding the lines represent 95% confidence intervals.

Intensities of aggressive acts by adult females

The model for intensity of female aggression was improved by including the random factor of ID ($\Delta\text{DIC} = -42$), indicating individual consistency between measures. Within this model only two factors appeared to significantly affect the intensity of aggressive acts displayed by adult females (Fig. 3a, b): females expressed more intense aggression in food-related contexts than in other contexts ($\text{pMCMC} < 0.01$) and when group sizes were larger than when they were smaller ($\text{pMCMC} < 0.01$). However, rank was not a significant predictor of aggression intensity ($\text{pMCMC} = 0.556$), nor were age ($\text{pMCMC} = 0.756$), proportion of lower-ranking targets present ($\text{pMCMC} = 0.156$) or relative prey density ($\text{pMCMC} = 0.289$).

Submissive Behaviour

For models predicting counts of unprovoked acts of submission we used data from 35858 observation sessions involving 136 females who had an opportunity to submit to at least one groupmate without first being attacked or threatened in each session. Overall, mean session length here was 46 min. As with the aggression count data set, the unprovoked submission count data set included zero

counts when at least one groupmate was present but the focal animal never submitted to it. Within these sessions we observed 4345 unprovoked submissive behaviours, and we used these to assess the intensity of submissive acts, approximately 17% of which were directed down the hierarchy and 83% of which were directed up the hierarchy. The mean number of opportunities per female to exhibit unprovoked submission during an observation session with at least one other groupmate present was 290 over her lifetime, with a range of 20–1141.

Counts of submissive acts by adult females

When the random factor of ID was included in the model predicting counts of unprovoked submissive acts by females, after controlling for session length, we found that ID improved model fit ($\Delta\text{DIC} = -200$). However, counts of unprovoked submissive acts were also related to context, age and rank (Fig. 4a, b, c). That is, the number of times adult females performed unprovoked acts of submission was higher in food-related ($\text{pMCMC} < 0.001$) and other ($\text{pMCMC} < 0.001$) contexts than at dens (Fig. 4a). Regardless of context, counts of submissive acts females performed per hour decreased as rank increased ($\text{pMCMC} < 0.001$; Fig. 4b), and females

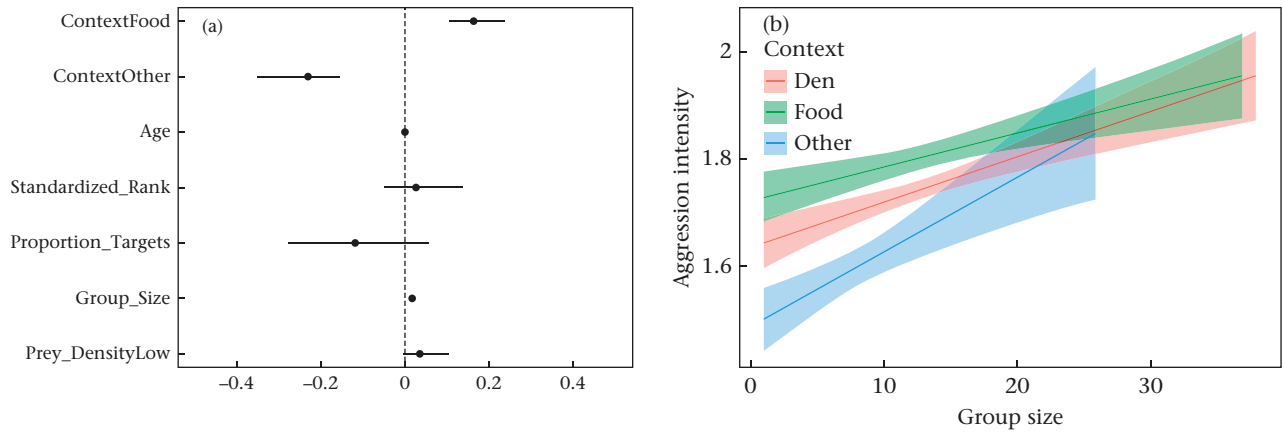


Figure 3. (a) Model assessing fixed predictors of intensities of aggressive acts performed by adult female hyaenas. (b) Mean intensity of aggressive acts performed by females in observation sessions taking place in different contexts based on the group size, or number of hyaenas present in an observation session. Coloured areas surrounding the lines represent 95% confidence intervals.

performed fewer submissive acts/h as they aged ($P < 0.001$; Fig. 4c). In contrast to our analysis of aggression counts, here we found no interaction between the proportion of targets present and group size, so the interaction term was dropped from the model. Group

size (pMCMC = 0.257), proportion of lower-ranking targets present (pMCMC = 0.777) and prey density (pMCMC = 0.314) had no significant effects on counts of unprovoked acts of submission, despite being included in the best model.

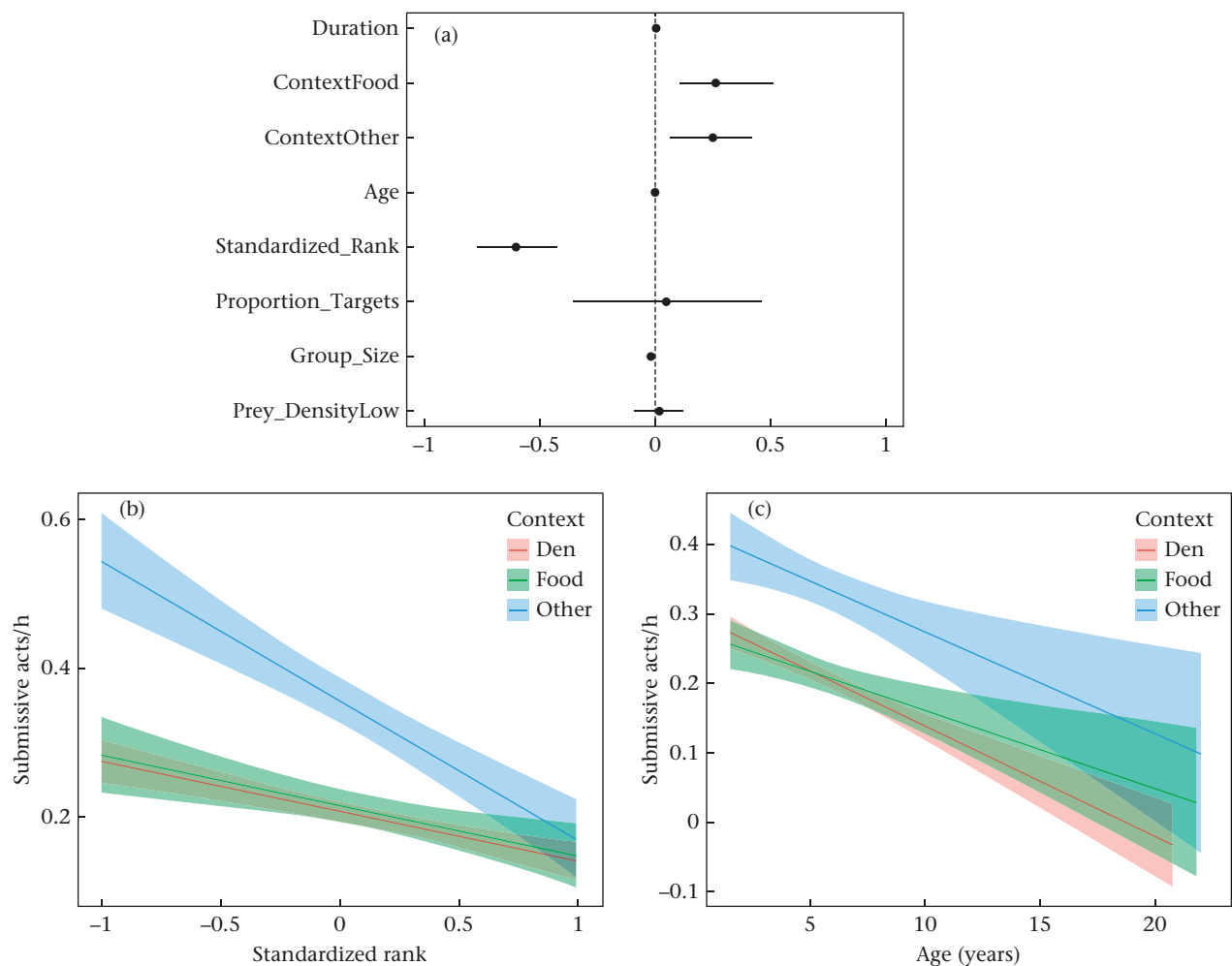


Figure 4. (a) Model assessing fixed predictors of the number of submissive acts performed by adult females. (b) Submissive acts performed by adult females/h (count/duration) in different contexts as a function of their standardized ranks. The shaded areas surrounding the lines represent 95% confidence intervals. (c) Submissive acts performed by adult females/h (count/duration) in different contexts based on the age in years of the individual in the observation session. The shaded areas surrounding the lines represent 95% confidence intervals.

Intensities of unprovoked submissive acts by adult females

As when modelling intensity of aggressive acts, the model predicting intensity of all submissive acts by adult females was improved by including the random factor of ID ($\Delta\text{DIC} = -35$). Females performed more intense unprovoked submissive acts during observation sessions with food present than during sessions in other contexts ($p\text{MCMC} < 0.001$; Fig. 5a, b). Rank also had a significant effect on the intensity of unprovoked submissive acts performed by females ($p\text{MCMC} = 0.04$). However, as in our analyses of intensity of aggressive acts, age had no significant effect on the intensity of submissive acts ($p\text{MCMC} = 0.318$), so this trait was consistent within individuals. The proportion of higher-ranking targets present with the actor also had no effect ($p\text{MCMC} = 0.449$), nor did group size ($p\text{MCMC} = 0.506$) or prey density ($p\text{MCMC} = 0.08$).

Correlation between Aggression and Submission within Individuals

As the counts of both aggressive and submissive acts were affected by both context and age, they were not consistent over time (Figs 2a, 4a), so these should not be considered personality traits; therefore, we did not assess the correlation between these two count measures. Indeed, counts of both types of behaviour appeared more closely related to social rank than to individual differences. However, as the intensity with which a female performed either aggressive or submissive acts remained consistent as she aged (Figs 3a, 5a), and as model fit was also significantly improved for both by adding the random factor of ID, we compared our two intensity measures to determine whether they were correlated. When we compared the mean lifetime intensities of aggressive behaviour to mean lifetime intensities of submissive behaviour within individuals, we found no correlation between intensities of these two types of acts ($P = 0.31$).

Fitness Consequences of Aggression and Submission

To assess correlations between each of our four agonistic traits and fitness, we ran separate models assessing the relationship between each mean trait value and the number of cubs produced in a female's lifetime that survived to 24 months. Models included mean lifetime rates and intensities of aggressive or submissive behaviours and mean lifetime rank. We found no significant interaction between mean lifetime rank and mean lifetime aggression rate in our model assessing the relationship between aggression counts, rank and fitness, so the interaction term was

dropped and this improved model fit. The effect of aggression count on offspring survival was not significant ($P = 0.284$), but social rank was highly and positively correlated with offspring survival ($P = 0.007$). We found a similar pattern with respect to the relationship between counts of submissive behaviour and offspring survival. The interaction between rank and submission rate was not significant, so the term was dropped. Submission rate was not correlated with offspring survival ($P = 0.217$), but rank was positively correlated with annual offspring survival ($P = 0.008$).

Interestingly, mean lifetime aggression intensity did show a pattern related to annual offspring survival. Within this model, mean lifetime aggression intensity had a polynomial relationship with annual offspring survival ($P = 0.001$), such that fitness was higher for individuals with midrange values of aggression intensity and lower for individuals on the extremes of the distribution, whereas rank presented a positive statistical trend with fitness in a linear relationship ($P = 0.06$). However, we did find a significant interaction between rank and aggression intensity in relation to annual offspring survival ($P = 0.002$). For individuals who had average lifetime intensities of aggressive behaviour closer to the centre of the distribution, as their rank increased, their annual offspring survival increased. However, for individuals presenting extreme average lifetime intensities of aggressive behaviour on either end of the distribution, increased rank did not show a significant positive correlation with annual offspring survival. As rank was not a predictor of aggression intensity in our individual consistency analysis (Fig. 3a), we chose to include an analysis comparing just lifetime aggression intensity to annual offspring survival, and here again, we found the relationship between the mean lifetime intensity and annual offspring survival to be significant ($P = 0.016$), presenting a polynomial relationship between annual offspring survival and mean lifetime aggression intensity independent of rank (Appendix, Fig. A1).

In our model assessing the relationship between mean lifetime submission intensity and annual offspring survival, we found a trending interaction between rank and submission intensity ($P = 0.07$). In this interactive model, individuals with lower average lifetime submission intensities showed a positive benefit of rank, but individuals with higher average lifetime submissive intensities did not show a positive benefit of rank. Within this model, rank was also positively correlated with fitness ($P = 0.0499$), but submission intensity was uncorrelated ($P = 0.864$). However, in a follow-up analysis in which we controlled for rank as Yoshida et al. (2016) did with aggressive behaviour, by only analysing intensity of submissive acts directed up the hierarchy, we did observe a significant

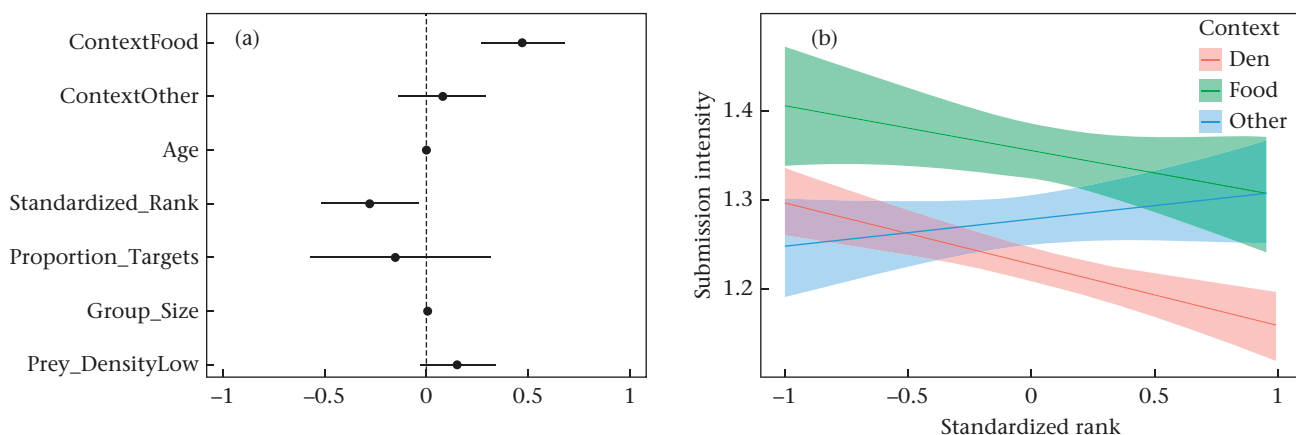


Figure 5. (a) Model assessing fixed predictors of intensities of unprovoked submissive acts performed by adult females. (b) Mean intensity of submissive acts performed by females in observation sessions based on their rank in the session taking place in different contexts. Coloured areas surrounding the lines represent 95% confidence intervals.

relationship between mean lifetime submission intensity and annual offspring survival ($P = 0.024$). Here again we found that fitness was lower on the extremes of the intensity distribution (Appendix, Fig. A2).

DISCUSSION

We found that the intensities, but not counts, of unprovoked acts of aggression and submission were consistent within individuals across time, suggesting that they represent true individual differences or personality traits. We found that the intensity of unprovoked agonistic behaviour varied strongly with context, with more intense aggressive and submissive behaviours occurring during feeding sessions than in other contexts. This is unsurprising given that aggressive competition over food is both intense and common in this species. Individual plasticity is clearly apparent in our data, given the important effects of rank, context and other factors on our behavioural measures. However, intensities of unprovoked aggressive and submissive acts did not vary with age among adult female spotted hyaenas (Figs 3a, 5a), and model fit was improved by including individual identity, suggesting strong consistency within individuals over time (Hadfield, 2010). Furthermore, although social rank clearly had effects on how often individuals performed aggressive or submissive acts, rank was not a significant predictor of the intensity of their aggressive acts, a result also obtained earlier by Yoshida et al. (2016).

Yoshida et al. (2016) did not assess submissive behaviour at all, but we found that rank had a significant effect on submission intensity. This appeared to be strongly related to contextual variation, such that lower-ranking hyaenas performed more intense submissive behaviours over food and at dens than elsewhere (Fig. 5b). Regardless, even in this model we observed individual consistency based on ID, and we did not see an effect of age, suggesting consistency within adults. This pattern warrants further investigation, but even so, we find it fascinating that intensity of agonistic behaviours seems to show true individual consistency across time. Similarly, Yoshida et al. (2016) found that aggressiveness was consistent over time within individual hyaenas, based on the intensity of their aggressive acts, but not on the rates at which they perform aggressive acts.

Based on the significant effects of rank, age, group size and proportion of targets present with the focal female on our count measures, we conclude that rank is likely the driving factor leading individuals to perform aggressive and submissive acts at higher or lower rates. Thus, social rank is positively correlated with the probability of performing aggressive acts (Fig. 2a) and negatively correlated with the probability of performing submissive acts (Fig. 3a). Although including ID improved model fit in analyses of counts of agonistic acts, suggesting some degree of individual consistency (Hadfield, 2010), age-related variation in count measures indicates considerably less consistency in these measures across time within individuals than in measures of intensity.

Our results also reveal that intensities of aggressive and submissive agonistic acts are not correlated within individuals. Our results thus support Nelson and Kriegsfield's (2017) hypothesis that an individual's aggressiveness is not necessarily predictive of its submissiveness when considering only unprovoked actions rather than those elicited by groupmates. They suggested that the intensity of an individual's aggressive and submissive acts may be largely independent of one another, which is inconsistent with the notion that these traits represent opposite ends of a single continuum. Our data also argue against the idea that aggressiveness and submissiveness are negatively correlated. Further analyses will be required to determine whether these traits are truly

independent of one another, as we can only discern clearly here that they are not correlated.

Mean lifetime rates of unprovoked aggressive and submissive acts did not appear to have any significant relationship to offspring survival when considered in the same model with effects of social rank. In all our analyses of fitness, the lifetime mean rank of the individual was strongly and positively correlated with annual offspring survival. It is interesting that rates of submissive, and especially aggressive, behaviour had no effects on fitness within our analyses, because this finding opposes an earlier result indicating that lifetime rates of aggressive behaviour are positively correlated with fitness (Yoshida et al., 2016). However, Yoshida et al. controlled for rank differently than we did here; they included as potential targets only the number of individuals of lower rank present with the actor in each observation session whereas ours included all clanmates present. Furthermore, their data set included only sessions in which at least one individual of lower rank was present in assessment of aggression, and they assessed only aggressive acts directed down the hierarchy. In contrast, our data set included all sessions in which two or more hyaenas were observed together, and we included acts directed both up and down the hierarchy.

Our results also differ in another important respect from those reported in earlier studies. Strauss and Holekamp (2020) conducted a study of coalitionary aggression by spotted hyaenas, where they found that only 6% of coalitionary attacks among adult females were directed up the hierarchy whereas 94% of such attacks were directed down the hierarchy, effectively functioning to maintain the status quo. Similarly, in earlier studies of dyadic aggression among adult male hyaenas (Holekamp & Smale, 1998) and adult female hyaenas (Smale et al., 1995), respectively, fewer than 3% of aggressive acts in dyadic interactions with clanmates were directed up the hierarchy and 97% were directed downward. By contrast, in the current study we found that 15% of aggressive acts were directed up the hierarchy, which seems surprising in comparison to the earlier studies. We believe that this is because, although all actors were adult females in our analyses, we included all acts of aggression directed against all clanmates present with the actor in observation sessions so long as their identity, age and rank were known. Similarly, we were surprised to find that 17% of submissive acts were directed down the hierarchy and 83% directed up the hierarchy. To assess the consistency of aggressiveness and submissiveness, we included all such behaviour occurring during observation sessions for which we had complete data. Our adult female subjects were thus able to attack or submit to any other clanmate, and our data set included cases in which adult females attacked cubs of higher-ranking females when their mothers were absent or appeased to lower-ranking animals.

Finally, we found that mean lifetime intensity of unprovoked aggressive acts was associated with reproductive success. In general, individuals whose mean lifetime aggression intensity measures represented extreme values on either end of the intensity distribution had lower offspring survival rates than did animals in the middle of the distribution, even though mean lifetime rank interacted with mean lifetime intensity of aggressive acts when included in the same model. Within this model it appeared that higher rank enhanced fitness for those individuals with mean lifetime aggression intensity values near the centre of the intensity distribution, but the benefit of higher rank was lost for individuals presenting extremely high or extremely low levels of aggression intensity. This polynomial relationship between mean lifetime intensity and annual offspring survival can be easily observed in Fig. A1 (Appendix). This figure and its related analyses highlight the detrimental effects of consistently presenting extreme levels of aggressive behaviour. On the other hand, individual submission

intensity did not appear to be correlated with fitness, as we observed no significant relationship between offspring survival and submission intensity unless we controlled for rank in the same way as done by Yoshida et al. (2016) (Appendix, Fig. A2). These patterns warrant more investigation, particularly given that we did observe individual consistency across time in the intensity with which females performed acts of aggression and submission.

It has been postulated that personalities in many nonhuman animals involve fitness trade-offs (Smith & Blumstein, 2008), and in humans it has been shown that extreme personality traits have costs (Gutierrez et al., 2013). Similarly, among nonhuman primates, extremely aggressive individuals suffer reproductive costs (e.g. Alberts et al., 1992; Packer et al., 1995). Furthermore, individuals on the extremes of these trait distributions, particularly on the positive extreme, may be suffering additional physical costs (Lane & Briffa, 2017). It is possible that individual variation in unprovoked aggressive and submissive traits observed in female spotted hyaenas may buffer individuals somewhat from rank effects on fitness, perhaps by affecting social bond strength or access to resources, or by reducing social stress. In any case, it appears that stabilizing selection may favour adult female hyaenas whose aggressive and submissive behaviours fall in the middle range of their respective spectra.

Author Contributions

S.K.M. cleaned and compiled the data, ran the statistical analyses and generated the figures and tables. K.E.H. contributed the field data, the ethogram and many of the relevant data collection methods. Both authors contributed to interpretation of the results and writing of the manuscript.

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Appendix

Agonistic Behaviours Expressed by Spotted Hyenas

Unprovoked aggressive behaviours

Stand over (st ov): t1. One animal stands with head high and muzzle pointed down towards the shoulders of another individual. Lower intensities of this behaviour may involve an approach with head up and ears forward, sometimes with tail bristled, which we refer to as 'pointing' (see below).

Point (pt): t1. A young hyaena adopts the exact same posture as an adult who is standing over another, but it is too small or too far away to put its head over the back or shoulders of the conspecific against which it is behaving aggressively. Point is used instead of 'stand over' whenever a youngster is too small to physically stand over the other animal or when the aggressor is approaching with head up and ears forward.

Head wave (hewa): t1. This is an intention movement to bite or lunge in which the aggressor moves its head unidirectionally towards the opponent to signal that it will escalate its aggression if the opponent hyaena persists in its current behaviour. The amount of movement is what differentiates this from a lunge.

Push: t2. One animal uses its body to push another.

Lunge: t2. One hyaena, often with ears cocked forward, suddenly moves quickly towards another hyaena, as if to bite; this may be done from either a standing or a lying position.

Chase: t2. Running pursuit. Note that a chase can also be a t3 if it ends in a tackle or if there is any other form of physical contact.

Snap: t2. Aggressor closes mouth rapidly near a conspecific, often making a snapping noise, but without any physical contact. Recorded as snap, not as 'attempt t3 bite'.

Bite: t3. One animal's teeth make physical contact with another hyaena. Multiple bites that occur in rapid succession during a single aggression are considered one t3 bite.

Bite shake (bsh): t3. One animal grips the skin of the back or shoulders of another with its teeth and violently shakes its head from side to side, sometimes with an upward pulling motion.

Unprovoked submissive behaviours

Back off (bo): s1. The animal withdraws a step or two from a particular individual but does not run or flee.

Ears back (eb): s1. Ears are flattened against the sides of the head. The more extreme the appeasement, the more radically the ears are flattened, but any clear flattening of the ears is recorded as a signal by one hyaena to another indicating that it perceives itself as subordinate to the other hyaena.

Head bob (hb): s1. Head wagging up and down or sideways.

Grin: s2. Retracting the lips to reveal the teeth, but the mouth is not open.

Open mouth appease (oma): s2. One animal puts its open mouth up to another animal's mouth. An open mouth appease involves the same motor patterns as a defensive parry but occurs spontaneously rather than in response to aggression.

Submissive posture (sp): s2. An animal stands or walks with its head lowered, body hunched and bent around towards a recipient, with butt tucked under and tail down between the legs. This often, but not always, occurs in conjunction with ears back and lips retracted in a grin.

Run/flee: s2. An animal runs from another individual or moves swiftly two or more body lengths away. (Note: this behaviour is usually, but not always, elicited by aggression; all instances are triple checked to be sure they are clearly not elicited by preceding aggression.)

Carpal crawl (cc): s3. A threatened animal crawls on its front carpal joints, with hindlegs bent (also known as 'grovel').

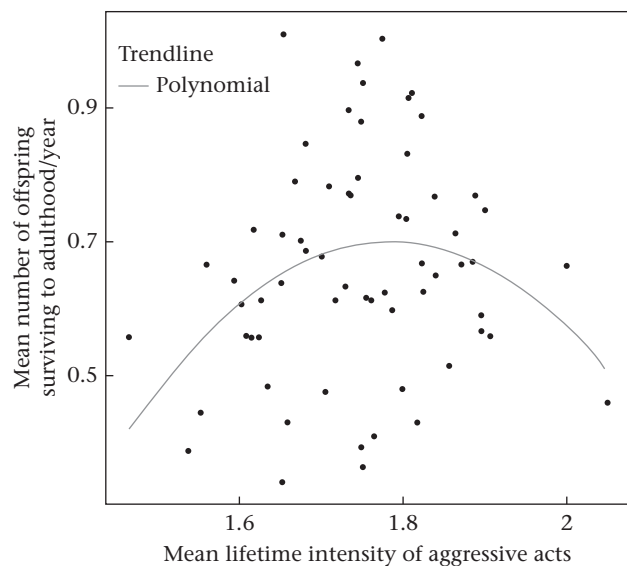


Figure A1. Lifetime reproductive success (number of cubs born that survived to 2 years of age) in relation to the mean lifetime intensity of aggressive acts performed by individual female hyaenas. The best-fit line for the distribution was a quadratic polynomial.

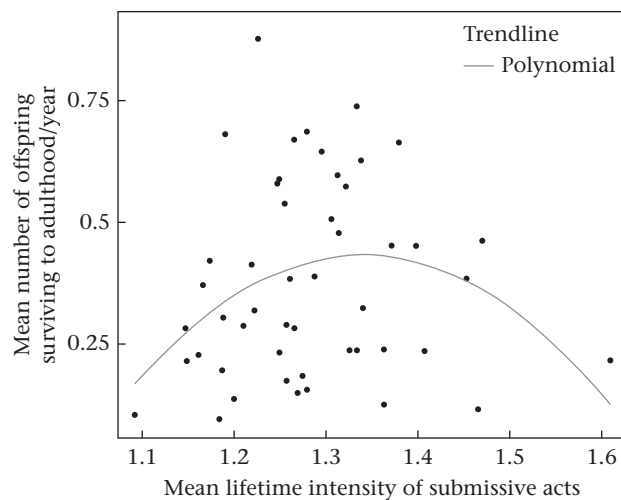


Figure A2. Lifetime reproductive success (number of cubs born that survived to 2 years of age) in relation to the mean lifetime intensity of submissive acts performed by individual female hyaenas up the hierarchy. The best-fit line for the distribution was a quadratic polynomial.