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ORIGINAL ARTICLE

Endurance rivalry among male spotted hyenas: what does it mean to "endure"?

Leslie J. Curren[1] · Maggie A. Sawdy[2,3] · Kim T. Scribner[2,3,4] · Kenna D. S. Lehmann[5] · Kay E. Holekamp[2,3]

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Abstract

In traditional definitions of endurance rivalry, individuals compete to remain reproductively active longer than their rivals, but these time periods are typically brief, such as a single breeding season. Here, we explored endurance rivalry among adult males in a long-lived species that breeds year-round, the spotted hyena (*Crocuta crocuta*). We found that most dispersing males navigated the adaptive challenges of remaining in their new clans ("enduring") for over 2 years before siring their first cub. Additionally, sires remained in their new clans at least 4 years, whereas males that never sired any cubs typically disappeared by their fourth year of tenure. This suggests that males might incorporate their initial reproductive success in the clan into their decisions regarding whether to "endure" by remaining in the current clan or to disperse again to another clan. Finally, we used Bayesian mixed modeling to explore variation in annual male reproductive success, which we found to have a positive linear relationship with tenure and a quadratic relationship with age. A male's rate of social associations with adult females, but not aggressive interactions with those females, was predictive of his annual reproductive success. We also found substantial individual variation in annual reproductive success across males. Our results support the notion that male spotted hyenas compete via an extended endurance rivalry; tenure unequivocally improves male reproductive success, but advanced age does not, and questions remain regarding other traits that might be salient to the rivalry or to female mate choice in this species.

Significance statement

Some animals compete indirectly for mates by trying to outlast their competitors during a finite breeding season; individuals that can endure the longest in this "marathon" reap the reproductive rewards. Male spotted hyenas face a different challenge because females breed year-round, so the competition to remain viable as mates is seemingly endless. Here, we show that male spotted hyenas seem to make decisions about whether to stay in a clan based on their initial reproductive success in that clan. For males with early success, the longer they stay and the more time they spend with females, the more cubs they sire each year. Our findings suggest that male spotted hyenas compete for mating opportunities via an "ultramarathon" in which they must remain in a single social group at the bottom of the hierarchy for many years to demonstrate to females their ability to endure.

Keywords *Crocuta crocuta* · Endurance rivalry · Male reproductive success · Spotted hyena · Tenure

Introduction

When one sex has a limiting reproductive rate, the other sex typically competes via at least one of four mechanisms of intrasexual competition: contest competition, scramble competition, sperm competition, or endurance rivalry (Andersson 1994). "Endurance rivalry" has traditionally referred to competition among males to remain reproductively active for as long as possible within a single breeding season and/or at a specific breeding site, with females demonstrating

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✉ Leslie J. Curren
leslie.curren@unh.edu

Extended author information available on the last page of the article

a mating preference for the winners of these "marathons" (Judge and Brooks 2001; Lidgard et al. 2005; Higham et al. 2011; Deakos 2012; Botto and Castellano 2016; Ospina-L et al. 2017). In the classic examples of endurance rivalry (e.g., Judge and Brooks 2001; Castellano et al. 2009), the outcome of competition relies heavily on fat and energy reserves and physical stamina (Mitchell 1990; Ospina-L et al. 2017; Vervoort and Kempenaers 2020). Males that enter the breeding season with the best body condition typically outperform rivals in the relevant measure (e.g., calling duration), but this exertion reduces these superior males to the poorest body condition by the conclusion of the breeding season (Bercovitch et al. 2003; Hoffman et al. 2008; Higham et al. 2011; Crocker et al. 2012; Petersen et al. 2021). Here we explore the possibility that male spotted hyenas (*Crocuta crocuta*) compete to reproduce via a protracted endurance rivalry that spans multiple years rather than a single breeding season.

Spotted hyenas are gregarious carnivores that live in social groups called clans. Although hyena clans have much greater fission–fusion dynamics than most primate groups with respect to both group size and structure, hyena clans resemble troops of macaques or baboons far more closely than they resemble groups of other mammalian carnivores (Holekamp et al. 2007). Clans may contain well over 100 individuals (e.g., Green et al. 2017); each clan contains one to several matrilines of adult females and their offspring, and 1–20 + immigrant adult males. Mean relatedness among natal animals from different matrilines is extremely low, meaning that clan-mates must compete and cooperate with unrelated animals as well as with their close kin (Van Horn et al. 2004). Each clan is structured by a linear dominance hierarchy (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986; Mills 1990), and an individual's position in the hierarchy determines its priority of access to food (Kruuk 1972; Tilson and Hamilton 1984; Frank 1986). Adult females are socially dominant to all adult males not born in the clan (Smale et al. 1993; Smale et al. 1997). Before cubs reach reproductive maturity, they attain ranks in the clan's dominance hierarchy immediately below those of their mothers (Holekamp and Smale 1993; Smale et al. 1993), and both male and female cubs typically maintain those ranks as long as they remain in the natal clan.

Hyenas of both sexes reach reproductive maturity at 24 months of age (Glickman et al. 1992). The vast majority (97%) of males engage in natal dispersal 1–5 years after they become reproductively mature (Smale et al. 1997; East and Hofer 2001; Honer et al. 2007), resulting in two classes of adult males in every clan: adult natal males that have not yet dispersed and immigrant males that were born elsewhere. Natal males often comprise over 20% of the adult male population, yet they sire only 3% of cubs, whereas immigrants sire 97% (Engh et al. 2002), so natal dispersal functions as a mechanism for inbreeding avoidance (Smale et al. 1997; Honer et al. 2007). This reproductive advantage to immigrants accrues despite the fact that immigrants are socially subordinate to all adult natal males because immigrants enter a clan at the very bottom of the linear hierarchy (Holekamp and Smale 1998). Immigrants' ranks are based strictly on their arrival order in the new clan, so immigrants improve their social status by queuing, such that an immigrant's rank only improves as he moves up the male queue due to death or secondary dispersal of males that arrived before him (Smale et al. 1997; East and Hofer 2001).

The mating system of the spotted hyena is promiscuous, such that both males and females typically mate with multiple partners. Among females, this commonly occurs even within a single bout of reproduction: 21–35% of twin litters are sired by multiple males (Engh et al. 2002; East et al. 2003). High-ranking immigrant male spotted hyenas do not monopolize reproduction as they do in many primates (e.g., Vigilant et al. 2015; Higham et al. 2021); previous work suggested that social rank accounts for only 18% of the variance in the reproductive success of immigrant male hyenas, but tenure accounts for 60% (Engh et al. 2002). Whereas in many primate species young adult males also disperse and must survive in subordinate rank positions for lengthy periods as they queue for better status (e.g., van Noordwijk and van Schaik 2001; Alberts et al. 2003), their reproductive success improves as their rank increases. In contrast, previous work found that the highest-ranking and the lowest-ranking immigrant male hyenas both have lower annual reproductive success than mid-ranking males (Engh et al. 2002), although those results did not account for male age. This may explain why roughly 40% of immigrants in our study population also engage in secondary dispersal (Van Horn et al. 2003), where males transfer between clans at least once again after joining their first new clan at natal dispersal.

Adult males of all ages may engage in secondary dispersal, so newly arrived immigrants span a wide age spectrum (Van Horn et al. 2003). We have opportunistically followed males born into one of our study clans as they transfer among as many as 4 different clans in their lifetimes (Smale et al. 1997; Van Horn et al. 2003). However, in addition to the high mortality risk associated with dispersing (Smale et al. 1997), each male engaging in either natal or subsequent dispersal joins their new clan's hierarchy at its very bottom, with the lowest priority of access to food (Smale et al. 1997; Holekamp and Smale 1998; East and Hofer 2001). Secondary dispersal is therefore a costly endeavor, and the reasons for its occurrence remain unknown. Here we inquire when immigrants first sire cubs after arriving in their new clan and use these data to test the hypothesis that males use initial reproductive success in the clan to make decisions about whether to secondarily disperse or remain in the clan, as is the case among various male primates (e.g., van Noordwijk and van Schaik 2001). Although we cannot usually assess directly whether males are engaging in secondary dispersal when they enter or disappear from our study clan, we can test the prediction of our hypothesis that a male's initial reproductive success in the clan should predict his total tenure in the clan.

In most endurance rivalries described in the literature, females demonstrate a mating preference for the winners of what are effectively "marathons" among competing males throughout the breeding season. Spotted hyenas initially appear unlikely candidates for this type of endurance rivalry because they have no annual breeding season; instead, they breed throughout the year (Kruuk 1972; Holekamp et al. 1999). Furthermore, they can live up to 26 years, so the "marathon" that a male hyena must endure would appear to be virtually endless. Whereas male long-tailed macaques (*Macaca fascicularis*) attain alpha male status in their queues, on average, after only 25 months (van Noordwijk and van Schaik 2001), male spotted hyenas do not achieve alpha status, on average, until they have been in their new clan for 5–9 years (East and Hofer 2001).

On the other hand, if the concept of an endurance rivalry is broadened to include persistence or survival over longer periods than a single breeding season, as was recently suggested by Shuker and Kvarnemo (2021), other factors make an endurance rivalry seem quite plausible. Female spotted hyenas have the limiting reproductive rate (Holekamp et al. 1996), and their full cooperation is required for successful intromission (Glickman et al. 2006). Male hyenas show considerable reproductive skew (Engh et al. 2002), so male-male competition should theoretically be intense in this species (Darwin 1871). Nevertheless, male hyenas do not meet the criteria for scramble competition (Andersson 1994), and combat between male rivals is an ineffectual mode of sexual selection in this species (East and Hofer 2001; McCormick et al. 2022). Sperm competition remains a potential mechanism for intrasexual competition among male spotted hyenas (Curren et al. 2013), but they may also compete via an endurance rivalry that requires much more stamina than that needed to last through a discrete breeding season (Judge and Brooks 2001; Lidgard et al. 2005; Higham et al. 2011; Stone 2014; Ospina-L et al. 2017; Vervoort and Kempenaers 2020; Petersen et al. 2021).

Although body size and social rank account for little of the variance in male reproductive success in this species (Engh et al. 2002), previous research has shown that tenure in a male's new clan after dispersal, regardless of whether this is natal or subsequent dispersal, may be an important component of an immigrant's reproductive success and one that reflects how long males must endure after dispersal before females start choosing them as mates (Engh et al. 2002; East et al. 2003; Honer et al. 2007). However, the magnitude and exact nature of this effect remain unclear. For example, East et al. (2003) found that males typically must wait 2 years in the clan before siring cubs, but the precise distribution of tenure at first paternity was not reported. It is currently unclear how an immigrant's reproductive success in the early years of his tenure might affect his decision to remain in the clan versus engaging in secondary (or subsequent) dispersal. It is also unknown how a male's age plays a role in his reproductive success. Therefore, here we explore the effects of male age and tenure on annual reproductive success to inquire whether male spotted hyenas compete for reproduction by enduring years of waiting near the bottom of the clan's hierarchy until females start choosing them as mates. The unusual external genitalia of the female spotted hyena make coercive sex impossible (East et al. 1993), so female choice is paramount in determining a male's reproductive success (Engh et al. 2002).

If adult male hyenas do compete via an endurance rivalry, we would expect to see a positive linear relationship between tenure and annual reproductive success (hereafter annual RS). Engh et al. (2002) explored reproductive success as a function of tenure and reported a significant positive effect of tenure, but their data hinted at a more complex relationship in which the longest-tenured males have very low annual reproductive success (see their Fig. 6). These data did not include male age, however, and work in other mammals, such as the American black bear (*Ursus americanus*; Costello et al. 2009) and white-tailed deer (*Odocoileus virginianus*; Newbolt et al. 2017), suggests that advanced age may temper the benefits of tenure (Johnson and Gemmell 2012). East et al. (2003) reported that some males have a "period of genetic reproductive inactivity" toward the end of their tenure and speculated that this could be due to reproductive senescence in fertility (but see Curren et al. 2013), but similar to Engh et al. (2002), they were unable to directly assess age effects. Here, we attempted to fill this gap in the literature by integrating both age and tenure in our exploration of male reproductive success.

Importantly, there may be additional components of endurance beyond a male's mere presence in the clan. We therefore explored other variables that might affect an adult male's reproductive success. Specifically, we tested hypotheses suggesting that two types of interactions with females also affect a male's decision regarding whether to remain in his new clan or transfer to a new one. First, endurance might entail not only being present in the clan, but also spending time in close proximity to adult females (Bercovitch 1997; Szykman et al. 2001; Keogh et al. 2012; Stone 2014) in order to develop affiliative relationships with them, as suggested by East et al. (2003). This hypothesis predicts that, when rank and tenure are controlled, a male's annual RS should increase as his associations with adult females increase (Bercovitch 1997). Second, Szykman et al. (2003) suggested that aggressive interactions between males and females might affect mate-choice decisions made by female spotted hyenas. Therefore, we also tested the hypothesis that endurance for male hyenas requires not only remaining in the clan for an extended period and associating closely with females, but also actively engaging in aggressive interactions with females (East et al. 2003; Keogh et al. 2012). This hypothesis predicts that we should see a significant relationship between a male's annual RS and the rate at which he directs aggression toward, or receives aggression from, adult females.

Methods

Subject population

The data analyzed here came from a large clan of spotted hyenas that was monitored continuously from 1988 to 2009 in the Talek region of the Masai Mara National Reserve, Kenya. We used unique spot patterns and other markings to identify individuals (Frank 1986), and we determined the sex of each individual based on the morphology of the glans of its erect phallus (Frank et al. 1990). The birthdates of all natal animals were estimated (± 7 days) using methods described previously (Holekamp et al. 1996), and for other individuals, we estimated age (± 6 months) from tooth wear (Van Horn et al. 2003). We considered a female to be an "adult" when she had reached 36 months of age or conceived her first litter, whichever occurred first (Smith et al. 2007).

On the rare occasions when a male remains in his natal clan throughout his adult life such that he never disperses, he may then sire offspring in his natal clan (East and Hofer 2001; Honer et al. 2010), although this is uncommon (Engh et al. 2002). In our study population, only 2 out of 307 natal males failed to disperse after reaching maturity (A. Booms and KEH, unpublished data). As has been described in other study populations (East and Hofer 2001), these two adult natal males behaved like immigrant males except that they were the highest-ranking males in the immigrant queue. We observed these two adult natal males attempting to mate with females and each successfully sired multiple cubs. Therefore, we included these two adult natal males in all our analyses; hereafter, "adult males" will include both immigrants and these two adult natal males.

We elected to include tenure rather than social rank in our analyses because the two parameters are highly correlated (Smale et al. 1997; East and Hofer 2001), but tenure contains additional information about an individual's life history and "endurance" in the clan, and previous work indicated that it is a better predictor of male reproductive success (Engh et al. 2002). Because we assessed reproductive success on an annual basis using calendar years, we assigned each adult male a "rounded tenure" and "rounded age" for each year in which he resided in the clan. For rounded tenure, if an adult male's arrival date in the clan was between January 1 and June 30, we assigned him tenure = 1 for that year, and the next calendar year was tenure = 2, etc. If his arrival date in the clan was between July 1 and December 31, we did not assign him a tenure for that year, and his first official year of tenure (tenure = 1) was the following calendar year. Tenure = 1 therefore reflects approximately the first 12 months of an immigrant's tenure; tenure = 2 represents months 12–24, etc. Likewise, for rounded age, if a male's estimated birthdate (Van Horn et al. 2003) was between January 1 and June 30, he was assigned age = 1 for the following year, but if his estimated birthdate was between July 1 and December 31, we assigned him age = 0 for the following year. For the two adult natal males that never dispersed, we began their tenure clocks on their second birthday, because male spotted hyenas achieve reproductive maturity late in their second year (Glickman et al. 1992). Each adult male was assigned a tenure for his final calendar year in the clan regardless of the month during that year in which he disappeared. We excluded from our analyses all adult males that arrived in the clan before the inception of the study in 1988, males that remained in the clan for less than 6 months, and males for which we lacked genetic data. Where appropriate, we report mean values ± standard error.

Behavioral data collection

All behavioral observations were conducted from vehicles for several hours each morning and evening around dawn and dusk. We initiated an observation session when we encountered a subgroup of one or more hyenas separated from others by at least 200 m (Smith et al. 2008). Because we were observing known individuals in the field, it was not possible to record data blind. At the start of a session, we first recorded the identity and activity of all hyena(s) present and then used all-occurrence sampling methods to record certain behaviors as critical incidents (Altmann 1974). These critical incidents included the following behaviors, which were all classified as "aggressive acts": bites, bite-shakes, chases, lunges, pushes, stand-overs, "points" (aggressive posturing), head waves, and displacements. We also recorded the identity and sex of each target of the aggression. We considered an aggressive act to be dyadic if there was only one aggressor and coalitionary if there were multiple aggressors cooperating to attack the same target.

To calculate annual rates of agonistic interaction between males and females, we first divided intersexual interactions into three categories: adult males directing dyadic aggression against adult females, adult males directing coalitionary aggression against adult females (also called "baiting"; Szykman et al. 2003), and adult females directing aggression (dyadic or coalitionary) against adult males. We elected to separate dyadic aggression by males against females from coalitionary aggression by males against females because previous research has suggested that female spotted hyenas might respond differently to these two types of aggression from males (Szykman et al. 2003). Then, for each session in which an adult male was present with at least one adult female, we counted how many times he directed dyadic aggressive acts toward females and how many times he was the target of aggressive acts by females. During each observation session in which an adult male was present with at least one adult female and at least one other adult male, we counted how many times he exhibited coalitionary aggressive acts against females. We then divided each count by the number of females present in the session to control for the number of opportunities to aggress or to receive aggression. Finally, we divided these numbers by the length of the session (limiting the analyses to sessions ≥ 15 min), thereby arriving at an hourly rate of each type of aggression in each session for each adult male present. We then averaged each of these three rates for each male across all sessions during each calendar year. In these calculations, we only included years in which a male was seen with an adult female (and, in the case of the rate of coalitionary aggression, with an adult female and at least one other adult male) at least ten times.

Genetic analysis of paternity

We collected DNA samples by anesthetizing individuals with Telazol (W.A. Butler Co., Brighton, MI, USA, 6.5 mg/kg) and extracting blood samples. We extracted DNA from blood using Puregene kits (Gentra Systems Inc., Minneapolis, MN, USA) and stored it in liquid nitrogen until it could be fully processed in the USA (Engh et al. 2002). We amplified and analyzed eleven autosomal microsatellite loci (CCr01, CCr04, CCr05, CCr07, CCr11, CCr12, CCr13, CCr14, CCr15, CCr16, and CCr17; GenBank Accession nos. AY394080-AY394084 and AF180491-AF180497) and one X-linked microsatellite locus (CCrA3; GenBank Accession nos. AY394085-AY394086) using conditions described previously (Libants et al. 2000; Engh et al. 2002).

To evaluate paternity, we first estimated the conception date of each natal animal by subtracting 110 days (the known gestation period; Holekamp et al. 1996) from each cub's birthdate. We calculated a conception period for each litter ranging from 6 months before to 2 months after, the date of conception. This broad range was a conservative estimate that allowed for uncertainty regarding a male's presence/absence in the clan and for errors in estimating conception dates. We considered potential fathers any immigrant, transient (present in the clan less than 6 months), or adult natal male unrelated to the litter's mother that were present in the clan during the conception period of a specific litter. Natal males were classified as unrelated to the mother when their coefficient of relatedness was < 0.125 based on known maternal genealogies; natal males were classified as adults if they were at least 36 months old by the end of the conception period, unless they never went on to disperse ($n = 2$), in which case they were considered adults at 24 months. We then assigned paternity to offspring using the program CERVUS (Marshall et al. 1998) with these input parameters: number of candidate fathers = 25 (90% of candidate fathers sampled, because we lacked genetic information for some candidate fathers), 88% of loci typed, and an input error rate of 1%. We only included individuals that had been genotyped at a minimum of six loci and only considered a male to be the father of an offspring when he was assigned paternity by CERVUS with 95% confidence. Because multiple paternity is common in spotted hyenas (Engh et al. 2002; East et al. 2003), we measured annual RS as the number of cubs sired per year rather than the number of litters.

Analyses of tenure at first paternity and tenure at disappearance

To inquire when immigrants first sire cubs after arriving in their new clan, we first created frequency distributions of males' tenure when they sired their first cubs. We also did this for numbers of adult males that disappeared during each tenure year without ever having sired any cubs. Then, to explore the relationship between reproductive success and adult males' tenure in the clan, we created density plots to compare the distributions of males that sired at least one cub and males that never sired any cubs at all. In this analysis, we excluded all males that had not yet disappeared by the end of the study period. We then used a survival analysis and Cox proportional-hazards model to determine if males that sired cubs in their first 4 years of tenure remained in the clan longer than males that did not sire cubs in their first four years of tenure. We included a censoring term in this survival analysis so we could retain the nine males that were still present in the clan at the end of the study period.

Exploring possible predictors of reproductive success with a statistical model

Here we modeled a male's annual RS, measured as the number of cubs to which he was assigned paternity in any given year. We created a Bayesian Markov Chain Monte Carlo generalized linear mixed model, assuming a Poisson distribution, with the R package MCMCglmm (Hadfield 2010). Because hyenas must become independent of the den to be darted, we only had genetic data for offspring that had achieved den independence, so this measure of reproductive success did not include cubs that died prior to den independence. To account for variation in the repeated measures we had for each male (one measure for each year during which he resided in the clan), we included a hyena's individual identity (ID) as a random effect in our model.

The fixed effects in our model reflected the variables that we identified as possible predictors of male reproductive success. First, to account for a possible relationship with age, we included a male's rounded age for the year in question with both linear and quadratic terms, the latter of which accounts for the possible reproductive senescence hinted at by previous work (Engh et al. 2002; East et al. 2003). We then included a male's rounded tenure for the year in question. Next, to address the possibility that social proximity to females is an additional component of endurance, we included the mean number of adult females present in sessions in which the male was observed. Then, to explore aggressive interactions as possible correlates of male reproductive success, we included the following fixed effects for each potential sire: the mean rate of dyadic aggressive acts he directed toward adult females per hour during a given year, the mean rate of coalitionary aggressive acts he directed toward adult females per hour during a given year, and the mean rate of aggressive acts (dyadic or coalitionary) he received from females per hour during a given year. Finally, we included how many total cubs were assigned paternity in a given year as a fixed effect to account for variation in the number of possible cubs a male might theoretically have sired during any given year. Because we could not assign paternity to any cubs sired in 1989, we excluded this year from the model. We standardized all continuous covariates (tenure, age, age^2, all three rates of agonistic interactions, and number of cubs assigned) to have zero means and unit variances before their inclusion in the model. Additional model specifications can be found in the Supplement.

For all fixed effects, we report the posterior mean estimates of the coefficients for each parameter, the 95% credible intervals (CI), and the *p*MCMC values. We considered a fixed effect to be statistically significant when its 95% CI did not overlap zero. We report the proportion of variance explained by the random effect relative to the total variance in the model, expressed as a percentage. We report all descriptive means with the standard error of the mean and the range. We used R v. 2.13.0 to conduct all statistical analyses (R Development Core Team 2013).

Results

There were 53 adult males for which we had genetic data that entered the clan after the start of our study period (1988) and remained in the clan for at least 6 months. Their mean age at entry into the clan was 3.7 ± 0.2 years (range: 1.6–8.6; $n = 49$). Of the 53 adult males for which we had genetic data, 43 disappeared before the conclusion of our study (2009). The mean length of tenure in the clan among these 43 adult males was 4.4 ± 0.4 years (range: 0.7–9.4), although the 10 males that were still present in the clan at the conclusion of our study included two males that exceeded this range: an immigrant with a tenure of 15 years at the conclusion of this study and an adult natal male with a tenure of 10 years.

Of the 250 offspring included in the paternity analysis, we were able to assign paternity at 95% confidence to 176 (70%) cubs, 172 (98%) of which had known, genotyped mothers. The mean observed error rate across all loci was 2.5%. We assigned paternity to 8.2 ± 1.1 cubs per year (range: 1–19), and each adult male sired an average of 0.6 ± 0.1 cubs per year (range: 0–5). Among the 53 adult males, 34 sired at least one cub during their tenure in the clan, and 19 never sired any cubs. On average, adult males were present in the clan for 2.4 ± 0.3 years (range: 0–8.2) before siring their first cubs (Fig. 1). Figure 1 also shows how many adult males disappeared during each tenure year without ever having sired any cubs.

Among the 43 males for which we had disappearance dates, the mean number of cubs sired during a male's lifetime tenure in the clan was 2.9 ± 0.6 cubs (range: 0–18). The 26 adult males that sired at least one cub during their tenure in the clan disappeared after a mean of 5.6 ± 0.4 years (range: 2.5–9.4), whereas the 17 adult males that never sired any cubs disappeared after a mean of 2.5 ± 0.4 years (range: 0.7–7.4; Fig. 2). In the Cox proportional-hazards model, fathering a cub in the first 4 years of tenure (Y/N) significantly predicted the male's tenure in the clan (Fig. 3, Sired coef = -0.68, $SE = 0.314$, $p = 0.03$, $n = 52$).

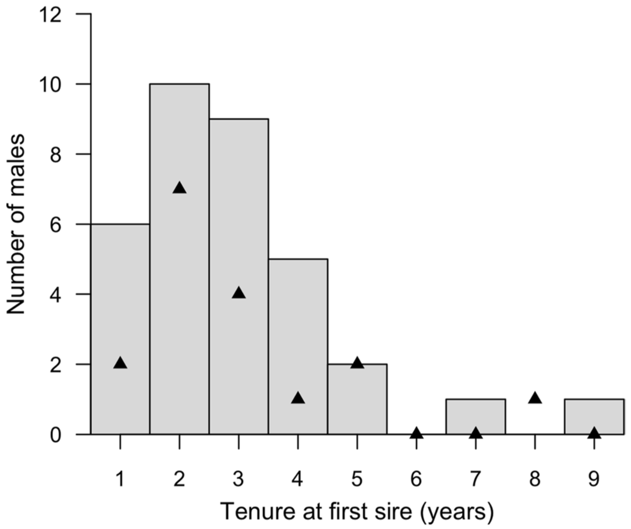

Fig. 1 A frequency histogram showing the tenure years during which adult male spotted hyenas (*Crocuta crocuta*) sired their first cubs (gray bars, $n = 34$). The black triangles indicate how many males disappeared during that tenure year without ever having sired any cubs ($n = 17$). Adult males were present in the clan for an average of 2.41 ± 0.29 years before siring their first cubs

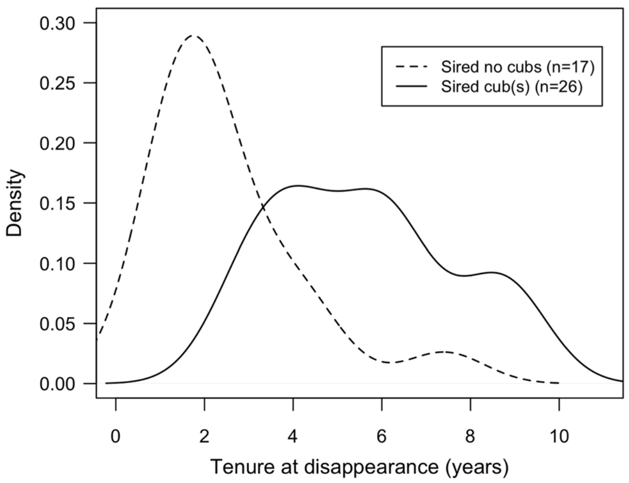

Fig. 2 A density plot showing the frequency distribution of tenure durations at disappearance among adult male spotted hyenas. The dashed line represents males that never sired any cubs, and the solid line represents males that sired at least one cub during their tenure in the clan. The two distributions are plotted with equal bandwidth

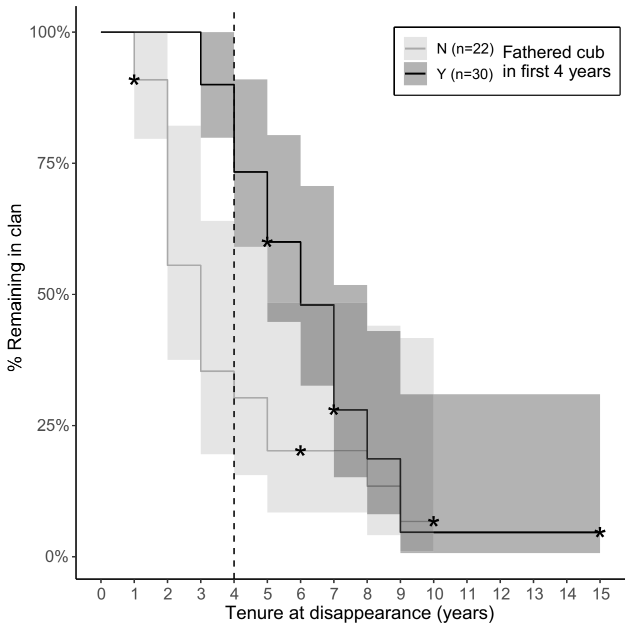

Fig. 3 Survival curves (solid lines) and 95% confidence intervals (shaded areas) comparing the tenure at disappearance for male spotted hyenas that did (black line) or did not (gray line) sire cubs within their first 4 years. The vertical dashed line indicates 4 years of tenure, and asterisks indicate males that were still present in the clan at the end of 2009 when this study concluded ($n = 9$)

The final model examined the annual RS of 48 individual adult males over the course of their lifetime in the clan (limiting our analyses to years in which a male was seen with an adult female at least ten times reduced the number of males from 53 to 48), resulting in 217 male-years. Removing the two adult natal males that never dispersed had no impact on the conclusions of the model (see Supplement Table S1), so we included them in the final model. The complete model results are reported in Table 1. We found a significant negative quadratic effect of age on annual RS, with a peak annual RS at age = 6.5 years (Fig. 4), and a positive linear effect of tenure on RS (Fig. 5). Although age and tenure are strongly correlated ($r = 0.85$), we had enough individuals with divergence between the measures to include both variables in our model and adequately estimate the marginal effects. We also found a significant positive relationship between the mean number of females present in each session with a given male and his annual RS (Fig. 6). There was no significant effect on annual RS of any of the three types of aggressive interactions (dyadic aggression directed by adult males toward females, coalitionary aggression directed by males toward females, or all aggression directed by females toward males). As expected, there was a significant positive correlation between the total number of cubs to which we could assign paternity each year and annual RS. Finally, hyena identity accounted for 29% of the total variance, suggesting that there are important individual differences beyond those included in our model.

Discussion

Here we found clear support for the idea that male spotted hyenas engage in an endurance rivalry wherein they must typically persist in the clan, with very low priority of access to food, for multiple years before achieving any reproductive success. We showed that an adult male spotted hyena must remain in a clan for an average of 2.4 years before siring his first cub (Fig. 1), so time present in the clan clearly represents an important part of the endurance contest among male spotted hyenas. Most adult males that sire cubs in a clan do so for the first time by their fourth year of tenure (Fig. 1), and the majority of these males remain in the clan for 4–8 years (solid line in Fig. 2). In contrast, adult males that never sire any cubs in the clan typically disappear 1–4 years after they arrive (dashed line in Fig. 2), and males that sired one or more cubs in their first 4 years of tenure remain in the clan longer than those that do not (Fig. 3).

The juxtaposition of Figs. 1, 2, and 3 may reveal a reproductive strategy previously undetected in spotted hyenas. Most males that eventually sire at least one cub in the clan do so within the first 4 years (Fig. 1), and most males that never sire any cubs disappear by the fourth year (Fig. 2, dashed line, and Fig. 3). One interpretation of these results is that perhaps a single factor is causing both a male's failure to sire offspring and his subsequent early disappearance from the clan, and future work should explore this possibility. Another interpretation, however, is that males are making

Table 1 Outputs of the Bayesian mixed model accounting for variance in annual RS of male spotted hyenas (*Crocuta crocuta*) using MCMCglmm ($n = 48$ hyenas). We report the posterior mean estimates of the coefficients of the fixed effects with 95% credible intervals (CI) and *p*MCMC values. Because the model uses the log-link function, the reported posterior mean estimates are log-scale coefficients and represent log-scale changes in the number of cubs sired per year relative to the intercept. Fixed effects presented in bold were considered significant because their 95% CIs did not overlap zero. All continuous covariates were standardized prior to their inclusion in the model

Variable	Posterior mean (95% CI)	*p*MCMC
Intercept	– 0.342 (– 0.694, 0.005)	-
Age	0.042 (– 0.537, 0.584)	0.874
Age^2	**– 0.685 (– 0.979, – 0.409)**	**< 0.0001**
Tenure	**0.622 (0.105, 1.164)**	**0.017**
Mean number of females per session	**0.263 (0.031, 0.496)**	**0.027**
Mean rate of dyadic aggressive acts directed by males toward females	– 0.020 (– 0.324, 0.264)	0.936
Mean rate of coalitionary aggressive acts directed by males toward females	– 0.225 (– 0.550, 0.088)	0.162
Mean rate of all aggressive acts received from females	– 0.060 (– 0.341, 0.211)	0.680
Total number of cubs assigned paternity in the year	**0.417 (0.179, 0.640)**	**< 0.001**
Random effect:	Proportion of variance:	
Hyena ID	29% (10%, 67%)	-

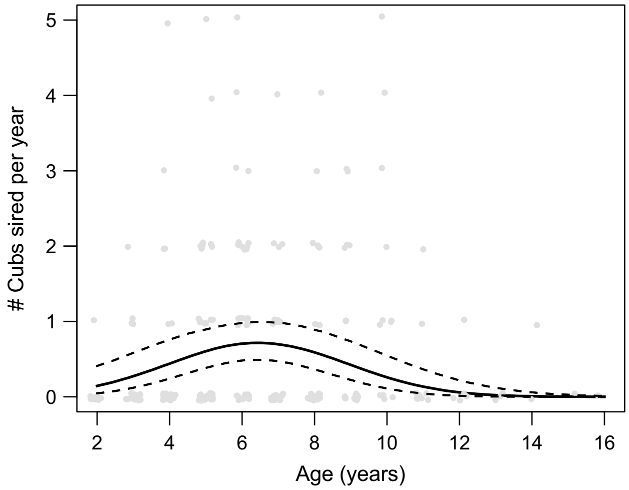

Fig. 4 The number of cubs an adult male spotted hyena sired per year as a function of his age. The solid black line represents the posterior mean estimate of the number of cubs a male sired per year generated by the model, the dashed lines represent the 95% credible intervals, and the gray points represent the raw data used to generate the model. The number of cubs sired per year peaks at the age of 6.5 years. Only cubs that reached the age of den graduation were considered in this analysis. These results correspond with those from the model presented in Table 1

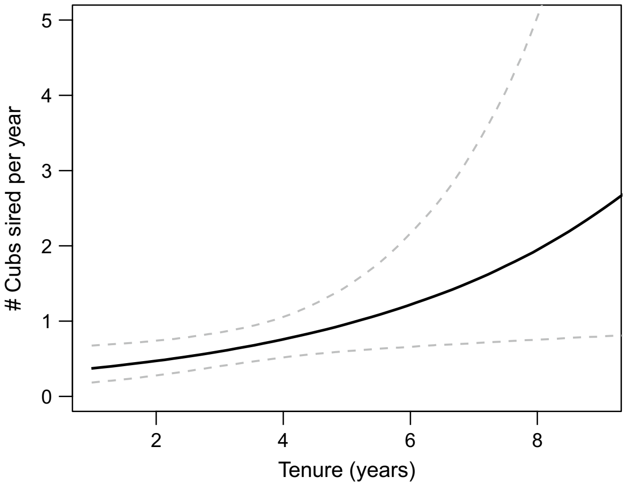

Fig. 5 The number of cubs an adult male spotted hyena sired per year as a function of his tenure in the clan. The solid black line represents the posterior mean estimate of the number of cubs a male sired per year generated by the model, and the dashed gray lines represent the 95% credible intervals. Only cubs that reached the age of den graduation were considered in this analysis. These results correspond with those from the model presented in Table 1, although in this Fig. (but not the model) we excluded tenure > 9 years due to the miniscule sample size ($n = 2$) at those advanced tenures

decisions regarding secondary or subsequent dispersal based on their early siring success in the clan. In contrast to that idea, Engh et al. (2002) found that adult males that remained in the clan for several years were no more likely to have sired cubs during their first 2 years of tenure than were adult males that disappeared during their third year of tenure, but their sample size ($n = 14$ males) was considerably smaller than ours ($n = 43$), and they examined siring success only during the first 2 years of tenure, rather than the first 4. Perhaps, then, males are indeed making decisions regarding secondary dispersal based on their early siring success in the clan, and the definition of "early" used by Engh et al. ("the first 2 years") was simply too narrow. The data we have presented here are consistent with this hypothesis.

The idea that males that have not sired a cub by their fourth year of tenure might then opt to disperse again is particularly intriguing because most males do not emigrate from their natal clan until they are between 2 and 5 years

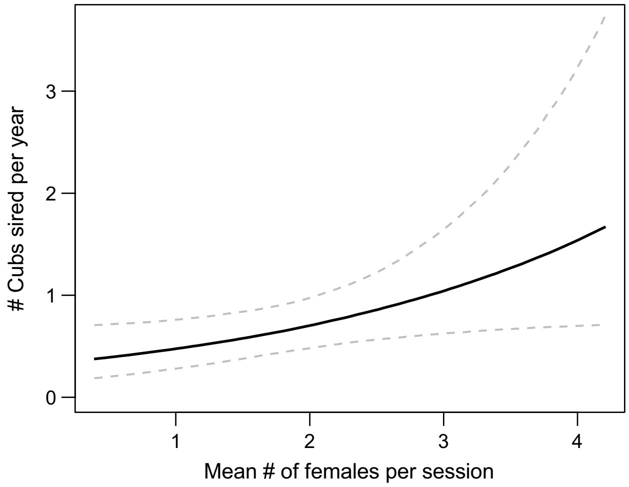

Fig. 6 The number of cubs an adult male spotted hyena sired per year as a function of his typical association with adult females. The solid line represents the posterior mean estimate of the number of cubs a male sired per year generated by the model, and the dashed lines represent the 95% credible intervals. Only cubs that reached the age of den graduation were considered in this analysis. These results correspond with those from the model presented in Table 1

old (Smale et al. 1997; Van Horn et al. 2003; Boydston et al. 2005) and rarely live longer than 15 years in the wild (Drea and Frank 2003). This means that adult males could be devoting as much as one-third (or, in many cases, close to half) of their post-pubertal lifespan to a reproductive effort that is ultimately fruitless before deciding to renew their effort in a different clan by dispersing again. In spite of this, theory predicts that the strategy of remaining in the clan to which they initially dispersed, despite not having early reproductive success, may still outperform secondary dispersal when the expected benefits of queuing and moving up in rank are enhanced by the increased survival benefits of remaining in the clan (Kokko and Johnstone 1999). These additional survival benefits (in this case, territory familiarity, better access to food, protection from rival clans and lions) become proportionally more significant in long-lived species like the spotted hyena, and in species in which secondary dispersal imposes great mortality risk, as it does among spotted hyenas (Smale et al. 1997; Kokko and Johnstone 1999). Despite these benefits of staying, our data indicate that very few males (8%) sire their first cub after 4 years of tenure (Fig. 1); at that point, dispersing again might be a better strategy despite its risks.

For males that sire cubs in their first 4 years in a clan, remaining in that clan may outperform secondary dispersal, but it still requires overcoming considerable challenges. Having just survived the high mortality risks associated with dispersing (Smale et al. 1997), a male must then endure the restricted food access that characterizes his new position at the bottom of a hierarchy containing as many as 125 other individuals (Green et al. 2018). As demonstrated here (Fig. 1) and by East et al. (2003), a male must typically survive these conditions for an average of more than 2 years before he obtains any reproductive benefits at all. Furthermore, to attain peak reproductive benefits, he must survive and remain in the clan even longer (Fig. 5). Our results therefore point to a contest among males to remain reproductively active for long periods of time, even though they may accrue no reproductive benefits during their first few years of tenure. Female hyenas may be selecting for longer tenured males, using endurance through these harsh conditions as an indicator of good genes and body condition (e.g., Darnell et al. 2020).

Interestingly, the quadratic relationship we found between age and annual RS (Fig. 4) suggests a more complex picture of male reproductive success, especially in light of the linear relationship between annual RS and tenure. Data from other mammals have shown a relationship between age and annual RS (e.g., olive baboons, *Papio anubis*, Packer 1979; red deer, *Cervus elaphus*, Clutton-Brock et al. 1988; northern elephant seals, *Mirounga angustirostris*, Le Boeuf et al. 2019; Barbary macaques, *Macaca sylvanus*, Kuester et al. 1995; see Takahata et al. 1999 for review). Decreases in annual RS are often ascribed to a decline in body condition with old age (Dunbar 1988; but see Bercovitch et al. 2003). The factors influencing body condition in spotted hyenas remain poorly understood, and there is little direct evidence suggesting that male body condition deteriorates after age 7, but Montgomery et al. (2022) found that lion mobbing behavior among immigrants peaks at the same ages (6–7 years) that we see annual RS peak here, so perhaps there is indeed a "prime age" for these males (Manson 1995). However, given that body condition does not affect social rank (and therefore access to food) or tenure among adult males (Smale et al. 1997; East and Hofer 2001), and given the near absence of paternal care in this species (Kruuk 1972), it is unclear how females could benefit from choosing prime age males over older males.

Alternatively, the decline in annual RS at advanced ages may be unrelated to female choice and instead be due to other negative effects of aging. For example, reproductive senescence due to fertility decline (the "paternal age effect"; Stene et al. 1977) is a possible explanation, although prior research found that ejaculate quality does not decrease with age in spotted hyenas (Curren et al. 2013); however, the sample size of older males in that study was very small. Perhaps males of "prime age" are better able to meet the physical challenges of copulation caused by the unique urogenital morphology of females in this species (Cunha et al. 2003). Regardless of the underlying mechanism, the quadratic effect of age on annual RS appears to favor males that can successfully emigrate out of their natal clan at younger ages (Höner et al. 2010), which would better position a male to benefit from the positive linear effect of tenure before encountering the negative effects of advanced age.

Future research should attempt to elucidate the mechanisms causing the decline in annual reproductive success for males older than 7 years. This includes determining the best indices of body condition in male spotted hyenas and then testing the hypothesis that male body condition affects annual reproductive success. In contrast to classic examples of endurance rivalries, in which males that enter a finite breeding season with larger energy reserves outperform other males (e.g., Higham et al. 2011; Crocker et al. 2012; Stone 2014; Ospina-L et al. 2017; Vervoort and Kempenaers 2020), male spotted hyenas do not store large energy reserves, perhaps because storage of such reserves as fat makes prey capture more difficult. Instead, hunting and scavenging ability may be more useful in helping them maintain good body condition, spend more time with females, and compete in an endurance rivalry that extends over many years.

The high degree of female control over copulation in this species (Cunha et al. 2003) suggests that female choice plays a significant role in male reproductive success. Here, we did not directly test female preferences, but we did explore factors in addition to age and tenure that might affect female mating decisions. We found that, after controlling for age and tenure, males that associated with a higher mean number of adult females had higher annual RS (Table 1; Fig. 6). Perhaps associating closely with more females is one way a male demonstrates his endurance in the clan, his regular presence serving as a reminder to females that he is overcoming the challenges of life at the bottom of a social hierarchy.

We found no support for the notion that a male's agonistic interactions with females influence his reproductive success. The rate at which adult females directed aggression toward a male did not affect his annual RS, nor did the rate at which the male directed dyadic aggression toward adult females. Most surprisingly, we found no relationship between the frequency with which a male directed coalitionary aggression toward adult females and his annual RS. Previous research pointed to a possible connection between aggressive coalitions of males baiting adult females and sexual selection, because females were the targets of these attacks more frequently when they were near the time of conception (Szykman et al. 2003), but our results are not consistent with that hypothesis. Perhaps these interactions are irrelevant to female mate choice in this species, and males associate with females purely to advertise their ongoing endurance and the good genes that contribute to it (Möller and Alatalo 1999; Botto and Castellano 2016).

Alternatively, perhaps affiliative, rather than aggressive, interactions between males and females affect male reproductive success (Szykman et al. 2001; East et al. 2003; Keogh et al. 2012; Rakhovskaya 2012). Richard (1992) found that female sifakas (*Propithecus verreauxi*) prefer males that act submissively toward them, and it is possible that female spotted hyenas exhibit similar preferences for males that demonstrate high rates of unsolicited appeasement behavior. And given that the random effect of male ID explained a large proportion (29%) of the variance observed in annual RS, there seem to be other individual-related factors contributing to male success that we did not measure here. One possibility is the male's rank in his natal clan, because Honer et al. (2010) found that sons of high-ranking females have higher reproductive success as immigrants, and maternal effects have been shown to enhance sons' reproductive success in other mammals (e.g., orcas, *Orcinus orca* Wright et al. 2016; bonobos, *Pan paniscus* Surbeck et al. 2019). Future analyses could also investigate whether a male spotted hyena's den attendance, interactions with cubs (e.g., Langos et al. 2013; Stadele et al. 2021), participation in territory defense (Boydston et al. 2001), display or courting efforts (East and Hofer 1991b; Szykman et al. 2007), relationships or relatedness with other males (Connor and Krutzen 2015; Stadele et al. 2015; Wikberg et al. 2018), or hunting and scavenging success influence his reproductive success. Vocal repertoire may also be relevant, given that male spotted hyenas spontaneously emit their long-distance "whoop" vocalization at higher rates than do females and that the male calls are highly variable in their complexity (East and Hofer 1991b; Theis et al. 2007). It has been suggested that this is to announce their location within the clan's territory (East and Hofer 1991a), but perhaps it is also to advertise their enduring presence in the clan, akin to the benefit we propose males accrue by associating with females (Fig. 6).

Shuker and Kvarnemo (2021) recently suggested a broad interpretation of "endurance rivalry" in which rivalries might span multiple reproductive events across an individual's lifetime. The data we have presented here support this expanded definition and indicate that endurance rivalry is an important mechanism of male-male competition in spotted hyenas, even though breeding occurs year-round in this species. Endurance rivalry among male spotted hyenas appears to be a multi-faceted contest, depending on a male's age, tenure in the clan, associations with adult females, and other individual differences. Future work should focus on elucidating female preferences in this species and determining the cause of the high individual variation that we have reported here.

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Data availability The datasets analyzed during the current study are available on Dryad at https://doi.org/10.5061/dryad.0vt4b8h2h.

Declarations

Ethics approval All procedures were approved by the Animal Care and Use Committee of Michigan State University. All applicable international, national, and institutional guidelines for the use of animals were followed.

Conflict of interest The authors declare no competing interests.

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Authors and Affiliations

Leslie J. Curren[1] · Maggie A. Sawdy[2,3] · Kim T. Scribner[2,3,4] · Kenna D. S. Lehmann[5] · Kay E. Holekamp[2,3]

[1] Department of Biological Sciences, University of New Hampshire, Durham, NH 03824, USA

[2] Department of Integrative Biology, Michigan State University, East Lansing, MI 48824, USA

[3] Ecology, Evolution, and Behavior Program, Michigan State University, East Lansing, MI 48824, USA

[4] Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA

[5] School of Biological Sciences, University of Nebraska-Lincoln, Lincoln, NE 68588, USA