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Sexual conflicts in spotted hyenas: male and female mating tactics and their reproductive outcome with respect to age, social status and tenure

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We investigated the reproductive outcomes of male and female mating tactics in the spotted hyena, *Crocuta crocuta*, a female-dominated social carnivore with high maternal investment, an absence of paternal care and female control over copulation. Paternity was determined using microsatellite profiling of 236 offspring in 171 litters from three clans. We found little evidence that male tactics that sought to coerce or monopolize females were successful. Polyandry and sperm competition appeared to counter effectively pre-copulatory male tactics, such as harassment, monopolization and other tactics, such as infanticide, that were against the evolutionary interests of females, and may have contributed to the stability of the male dominance hierarchy, which operated as a social queue. At least 39% of 54 females mated multiply, and 35% of 75 twin litters were fathered by two sires. Polyandry may also serve to ensure fertilization, compensate for an initial poor-quality mate or ensure fertilization by genetically compatible mates. Female mate choice matched observed patterns of affiliative male–female behaviour, indicating that affiliative behaviour is a successful male mating tactic, and was consistent with the idea that male tenure may serve as an index of male quality, although male fertility may decline with extreme old age.

Keywords: sexual conflict; sperm competition; multiple paternity; female mate choice; inbreeding; infanticide

1. INTRODUCTION

When maternal investment is high and paternal investment is low, sexual-selection theory predicts that females should exercise mate choice, because the benefits of being choosy are likely to be greater than the costs of mate choice, and that males should be less choosy (Trivers 1972; Parker 1983; Reynolds & Gross 1990; Clutton-Brock & Vincent 1991; Johnstone *et al.* 1996). When the evolutionary interests of males and females differ, sexual-conflict theory predicts that males should evolve traits that seek to manipulate female mate choice through direct and indirect male–male competition (Parker 1979) or harassment (Clutton-Brock & Parker 1995), and females should evolve counter-tactics against male manipulation (Parker 1979; Gowaty 1996; Moore *et al.* 2001).

In this study, we investigated the reproductive outcomes of female and male mating tactics among spotted hyenas, *Crocuta crocuta*, in the Serengeti National Park, Tanzania. A high level of sexual conflict was expected because maternal investment in small litters (singletons, twins or rarely triplets) is high, owing to the production of highly nutritious milk during a 12–18 month lactation period, and interbirth intervals are long (Hofer & East 1995, 2003). Spotted hyenas are particularly appropriate for an investigation of male mating tactics and female counter-tactics because hyena society is socially dominated by females, and, owing to the unusual anatomy of females (Matthews 1939), males require the complete cooperation of females during copulation (Kruuk 1972; East *et al.* 1993; figure 1).

Serengeti males exhibit several behaviours that are most probably aimed at manipulating female mate choice. These range from affiliative behaviour to harassment and attempted infanticide (see below), and generally these tactics are chiefly focused on high-ranking females (East & Hofer 2001; see also § 3d). High-ranking females are high-quality mates because their offspring grow at a faster rate, survive better and start to reproduce at a younger age than those of subordinate females (Hofer & East 2003). High-ranking males consort mostly with high-ranking females by 'shadowing' them, and males above median rank may 'defend' a female as a resource by excluding more subordinate males from her (East & Hofer 2001; Goymann *et al.* 2003).

In other species, males persuade females to be less choosy by harassing them (Clutton-Brock & Parker 1995; Connor *et al.* 2001; Fox 2002). In spotted hyenas, levels of male harassment vary from an individual male challenging a female to groups of males violently attacking a female (Kruuk 1972; East & Hofer 2001).

If shadowing, defending or harassment are effective tactics, males should sire progeny with the females they try

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Figure 1. During copulation males require the complete cooperation of females because of the unusual anatomy of female hyena genitalia, including an enlarged clitoris and the lack of a vulva. Urinary and genital tracts join to form a canal that passes through the clitoris with an opening at the tip of the clitoris directed downwards and towards the head. The male inserts his penis into the clitoris in a vertical fashion while perilously holding on to the back of the female.

to manipulate, and selection should favour such male tactics. If male tactics are detrimental to females, counter-tactics against male manipulation should evolve, and systematic variation in the level of manipulation applied by males to females of different ranks should influence the extent to which counter-tactics are employed.

Serengeti immigrant males acquire high social status by observing strict queuing conventions (*sensu* Kokko *et al.* 1998) for many years in queues that may contain more than 20 males (East & Hofer 2001). Despite this, queues are stable and physical contests between male hyenas are rare (East & Hofer 2001). It has been suggested that to be accepted as a mate, a male needs to develop a relationship with a female, and, because a relationship is a non-transferable resource, males stand to gain little from aggressive contests (East & Hofer 1991; East *et al.* 1993). This implies that female mating tactics may have curbed selection for overt male–male contests and contributed to the evolution and stability of the male social hierarchy (East & Hofer 1991, 2001, 2002).

By mating with multiple mates, females may counter male tactics that have negative fitness consequences for females (Eberhard 1998; Jennions & Petrie 2000), and, by preventing monopolization of paternity, females may increase social stability in species such as spotted hyenas where males queue for social status (Kokko & Johnstone 1999). Mating with multiple males would also favour post-copulatory male–male competition (Eberhard 1998) and may enhance female reproductive success through selection either of sperm of high quality (Madsen *et al.* 1992) or of genetically compatible sperm (Zeh & Zeh 1997).

Mating with multiple males and mixed paternity have been extensively studied in many insect and bird species, but little is known about this female mating tactic in social mammalian species (Jennions & Petrie 2000). The incidence of multiple-paternity litters among females of differ-

ent social statuses may therefore reflect the interplay between rank-related differences in the costs and benefits of mating with multiple males and female mate choice (Gowaty 1996). Competition between Serengeti males for access to dominant high-quality females (East & Hofer 2001) would provide the high-ranking females with low-cost access to many males (Parker 1983; Gowaty 1996; Johnstone *et al.* 1996), and thus dominant females would be expected to have a high incidence of mixed-paternity litters if the benefits of polyandry outweigh its cost. However, if the main benefit of mating with multiple males is to reduce the cost of producing offspring exclusively sired by low-quality males, then high-ranking females might be expected rarely to mate multiply, as they are unlikely to need to accept a low-quality male.

Using previously described patterns of association between males and females in three hyena clans (East & Hofer 2001), we predicted the distribution of paternity among males under the assumption that male mating tactics were successful and tested this prediction using observed paternity determined by microsatellite profiling of progeny.

2. MATERIAL AND METHODS

(a) *Study population*

Serengeti spotted hyenas live in stable multi-female multi-male fission–fusion groups, which contain natal adult females, immigrant adult males and rarely 'non-dispersing' natal adult males (Hofer & East 1993*a*; East & Hofer 2001). All females breed, producing litters throughout the year (Hofer & East 1995). We present data from the Isiaka, Pool and Mamba clans, which were studied for *ca.* 13 years (May 1987–December 2000), 11 years (November 1989–December 2000) and 10 years (August 1990–December 2000), respectively, and contained on average 12 (range of 6–20), 15 (range of 9–20) and 20 (range of 14–27) adult males and 20 (range of 14–24), 26 (range of 16–34) and 33 (range of 26–37) adult females, respectively. Clans defended group territories; all members were known individually (Hofer & East 1993*a*). All clan members regularly left the territory individually or in small groups on short-term long-distance foraging trips to concentrations of migratory herbivores, when migratory prey were absent from their territory (commuting system) (Hofer & East 1993*a–c*). Demography and behaviour were recorded during more than 15 000 hours of detailed field observations.

(b) *Behaviour, status, tenure and oestrus*

Using submissive responses in dyadic interactions, we constructed separate dominance hierarchies for adult females and immigrant males. To compare rank positions across clans, individuals were assigned a standardized rank by distributing ranks evenly between the highest rank (standardized rank $+1$) and the lowest rank (standardized rank -1), with the median rank being scored as zero. Individuals with standardized ranks within the top, middle and lower thirds of the total range were then classified as high-ranking, mid-ranking and low-ranking, respectively (East & Hofer 2001).

Male tenures refer to the duration of the period from the date of immigration until the event in question, usually the date of conception of a litter. Immigrant-male total tenure was the period between the date a male was first observed in a clan territory and the date he was last sighted. Censored tenures for immigrant

males that were clan members when observations commenced were excluded from the analyses. The adult tenure of males that did not disperse began when the male reached adulthood, which was set at 2 years of age (Hofer & East 1993*a*, 1995).

The date of conception was calculated from litter birth dates based on a gestation period of 110 days (Matthews 1939). Birth dates were either known or estimated from the pelage and behaviour of cubs and were likely to be accurate to within 7 days (Hofer & East 1993*c*). Female spotted hyenas are thought to have an oestrus period of 1 day and to cycle every 14 days (Matthews 1939; Schneider 1952).

Possible male manipulation tactics were classified as affiliative behaviour, shadowing, defending or harassment. Affiliative behaviour included grooming, greeting and other amicable gestures; shadowing occurred when males followed a female, and defending occurred when a male prevented other males from interacting with a female (for detailed definitions see East & Hofer (2001)). Low levels of harassment involved a male approaching a female aggressively, lunging at or biting the female or attempting to mount when the female did not cooperate (East & Hofer 2001). Intense harassment, termed baiting, involved coalitions of males attacking typically solitary females (Kruuk 1972). All incidences of males employing likely manipulative tactics were recorded *ad libitum*; multiple records on a particular day were excluded from the analysis.

(c) *Genetic analysis*

Microsatellite loci were typed using DNA isolated from blood ($n = 47$), other tissues ($n = 41$), skin biopsy ($n = 159$), the epithelial layer covering faeces ($n = 3$) and hair ($n = 221$). Results from hair and biopsy samples were compared for 45 individuals and found to be identical. Hair was plucked from cubs that walked close to our vehicle using pliers. By collecting hair we sampled 50% of cubs before they reached six months of age. Tissue samples were collected opportunistically from dead animals. Blood samples were collected in ethylenediaminetetra-acetic acid (EDTA)-coated tubes from immobilized animals following the procedure outlined in Hofer & East (1993*a*). Skin biopsies were collected using a Telinject GUT 50 dart gun fitted with a biopsy needle designed for spotted hyenas. Instruments used to collect genetic samples were sterilized and then held in the flame of a cigarette lighter before use. Genetic material was either stored and transported at or below $-70\,°C$, or stored in ethanol at $5\,°C$ (hair, tissue and biopsies).

Fluorescent primers were used to amplify six hyena microsatellite loci: *Ccroc*05, *Ccroc*09 and *Ccroc*10 (dinucleotide repeats), and *Ccroc*06, *Ccroc*07 and *Ccroc*08 (tetranucleotide repeats). The number of alleles ranged from 8 to 17 (mean of 12.5 per locus). For details of methods and primers see Wilhelm *et al.* (2003).

(d) *Paternity*

The paternity analysis included all immigrant and 'non-disperser' males (East & Hofer 2001) that were clan members when a litter was conceived. Clan membership included a 90-day period before and a 90-day period after the first and last dates on which immigrant males were sighted because commuting individuals may have been members before or after these sightings (Hofer & East 1993*a*). 'Non-dispersing' males were considered potential fathers from the age of 2 years until 90 days after they were last sighted before emigration. Paternity was assessed using maximum-likelihood methods as implemented in Cervus v. 2 (Marshall *et al.* 1998). The litters included in this analysis

($n = 171$ litters, 236 cubs) were all singletons or twins for which the sire or one of the sires was determined with 95% confidence. Mixed-paternity twin litters were those in which two sires were identified and at least one sire was allocated with 95% confidence. The tenure and social status of both males that sired mixed-paternity twin litters were included in the analysis. The mean expected heterozygosity was 0.856 ($n = 471$), the total exclusion power was 0.9996, the mean proportion of individuals typed was 0.972, and the error rate was 0.008 and was set at 1%.

(e) *Adjustment of potential bias towards males that sired offspring with high-ranking females*

As offspring survival was influenced by maternal status (Hofer & East 2003), offspring of dominant mothers were more likely to survive to the age at which we obtained a genetic sample (mean age of cubs when sampled was 7.32 ± 4.91 months). We deduce this from the fact that the numbers of cubs born to high-, mid- and low-ranking females (293, 226 and 263 cubs, respectively) did not vary from random expectation ($\chi^2 = 4.371$, d.f. $= 2$, $p = 0.112$), whereas the number of litters for which we established paternity with 95% confidence ($n = 171$) from high- ($n = 85$, 50%) mid- ($n = 39$, 23%) and low-ranking females ($n = 47$, 27%) did ($\chi^2 = 9.86$, d.f. $= 2$, $p = 0.007$). We adjusted the excess of litters of high-ranking females with known paternity by including 52 randomly selected litters from the 85 litters from high-ranking mothers, producing, for the three categories of female social status, relative frequencies of litters where paternity was determined that equalled the relative frequencies of litters at parturition (37.7%, 28.3% and 34.1% for high-, mid- and low-ranking females, respectively). We used this sample ($n = 138$ litters) in all analyses where we considered female choice across female rank categories, and refer to it as the 'adjusted sample'. By applying minimally invasive techniques, we obtained genetic samples from juveniles at a younger age than in studies that took blood samples from hyena cubs following anaesthesia (Szykman *et al.* 2001; Engh *et al.* 2002), and thus included an appropriate representation of sires of cubs born to low-ranking females in our sample.

(f) *Statistics*

Statistical analyses were performed using Systat v. 9.0 (SPSS Science Inc., Chicago, IL, USA) and StatXact v. 5.0 (Cytel Software Corp., Cambridge, MA, USA). All statistical tests are two-tailed. All means are quoted ± s.d. The significance of Spearman's rank correlations and Friedman tests were calculated for large sample sizes according to Siegel (1956) and for small sample sizes using exact *p* values with StatXact v. 5.0.

3. RESULTS

We identified 66 males as fathers with confidences of 95% for a total of 171 cubs; 22 males were not allocated any paternity with 95% confidence.

(a) *Male competitive ability and tenure*

There was no association between maternal and paternal standardized ranks in the adjusted sample (figure 2; Spearman's $r = -0.001$, $n = 138$, n.s.), indicating that dominant males did not monopolize paternity with dominant females. The mean social status of successful males in the adjusted sample was, however, significantly higher
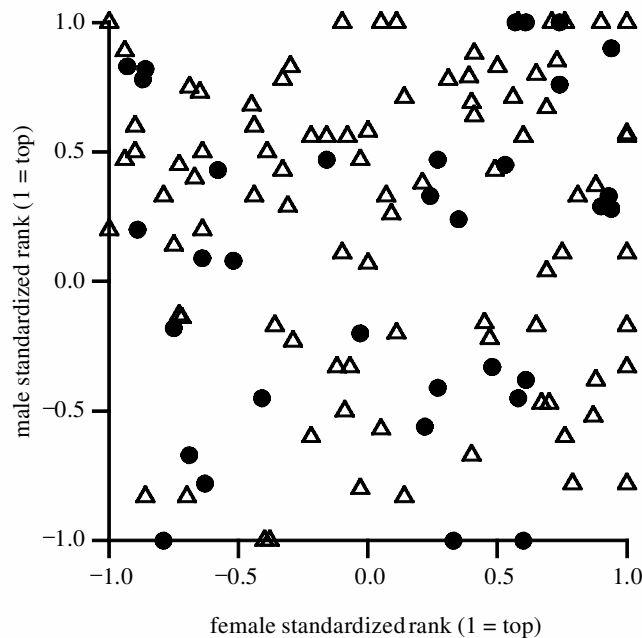
Figure 2. The standardized rank of fathers in relation to the standardized rank of mothers of spotted hyena litters. Filled circles, young females of less than 5 years of age; open triangles, old females of more than 5 years of age.

Figure 3. (*a*) Average proportion of cubs fathered (out of all cubs fathered by each male throughout his lifetime) and (*b*) average proportion of females with whom a male sired offspring (out of all females with whom each male sired offspring throughout his lifetime) increased with tenure. Period I, between 0 and 2 years of tenure; II, between 2 and 4 years of tenure; III, more than 4 years of tenure. Box, interquartile range around the median (central line inside the box); vertical lines outside the boxes cover values plus or minus 1.5 times the interquartile range; asterisks, single data points outside this limit.

than the median rank (0.19 ± 0.58, $n = 138$; one sample *t*-test: $t = 3.84$, $p = 0.0002$). High-, mid- and low-ranking females in the adjusted sample produced offspring with sires of similar average ranks (mean standardized ranks of sires for high-, mid- and low-ranking females were 0.23 ± 0.61, 0.18 ± 0.53 and 0.14 ± 0.59, respectively; Kruskal–Wallis test: $H = 0.818$, d.f. = 2, $p = 0.66$).

Males sired their first offspring 2.0 ± 1.4 years after immigration ($n = 47$). The mean tenure of sires in the adjusted sample was similar in all clans (Isiaka: 3.5 ± 1.4 years, $n = 41$ males; Mamba: 3.1 ± 2.1 years, $n = 28$; Pool: 3.3 ± 2.0 years, $n = 40$; Kruskal–Wallis test: $H = 1.727$, d.f. = 2, $p = 0.42$). As Serengeti males immigrated into the study clans at *ca.* 4 years of age (East & Hofer 2001), males with 3 years of tenure were *ca.* 7 years of age.

The number of cubs sired by males with total tenures exceeding 4 years in the adjusted sample (mean tenure of 6.8 ± 1.6 years) increased as their tenure progressed, with most progeny sired by males that held tenures of at least 4 years (10 litters sired by males tenured less than 2 years, 36 litters sired by males tenured between 2 and 4 years, and 56 litters sired by males tenured for 4 or more years; Friedman test: $T = 14.3$, d.f. = 2, $n = 19$ males, $p = 0.0009$; figure 3*a*). The number of different females with whom these males sired cubs also increased with male tenure (eight females for males tenured less than 2 years, 26 females for males tenured between 2 and 4 years and 46 females for males tenured for 4 or more years; Friedman test: $T = 15.31$, d.f. = 2, $p = 0.0005$; figure 3*b*).

For immigrant males that had tenures exceeding 4 years (and therefore had longevities likely to be above the average life expectancy (Hofer & East 1995)) and consequently reached high social status at the end of their tenure, including the alpha position in eight cases, we calculated a period of 'genetic reproductive inactivity' between the date on which the male ($n = 13$) fathered his
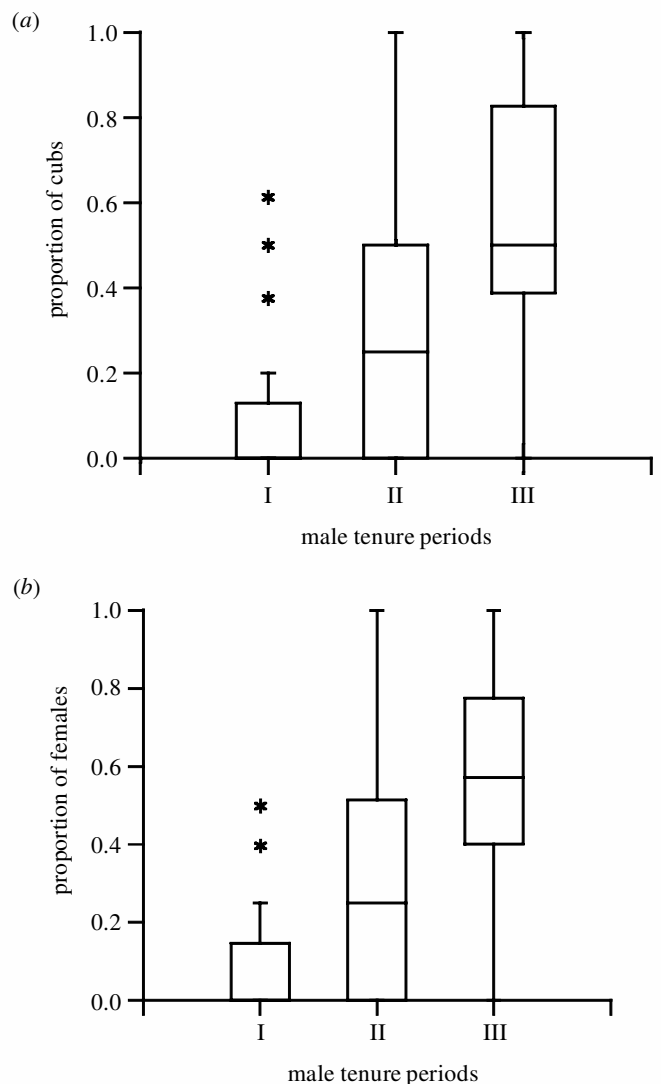
final litter and the last date on which the male was observed. As the duration of total tenure increased, the period of 'genetic reproductive inactivity' at the end of the tenure also increased ($r = 0.632$, $n = 13$, $p = 0.024$). The longest uncensored tenures of males in the Isiaka, Mamba and Pool clans on the day they sired their final litters were 6.2, 7.4 and 7.6 years, respectively.

Affiliative male–female interactions suggest that young females should prefer recent immigrants as mates and old females should choose longer-tenured males (East & Hofer 2001). Using the adjusted sample, we found such a positive correlation between female age and male tenure on the date of conception (figure 4; $r = 0.234$, $n = 81$, $p < 0.05$).
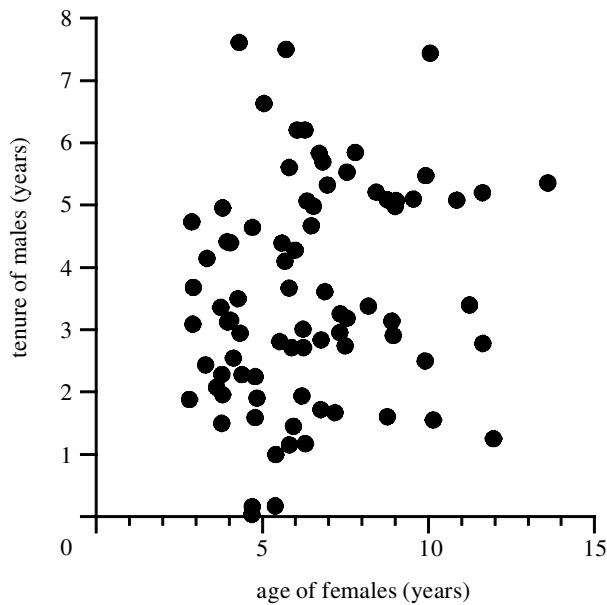
Figure 4. The duration of tenure of males when they sired a particular litter in relation to the age of the mothers on the date of conception.
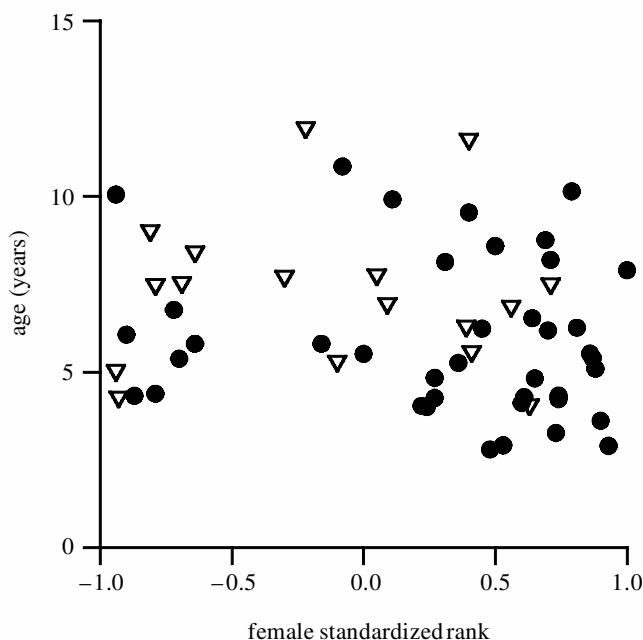

Figure 5. The relationships between maternal standardized rank, maternal age (years) and the incidence of twin litters in which both cubs were sired by one male (filled circles) and litters in which the two members of the litter were sired by different males (open triangles).

(b) *Multiple-paternity litters*

Out of 75 twin litters, 26 (34.7%) were sired by two males. Out of 54 mothers of completely sampled twin litters, 21 (38.9%) produced multiple paternity litters. A logistic regression demonstrated that the likelihood of producing a multiply sired litter declined with increasing maternal status and tended to increase with maternal age (figure 5; log likelihood: $G = 9.08$, d.f. = 2, $p = 0.011$; effect of female social status: $t = 2.16$, $p = 0.031$; female age: $t = 1.73$, $p = 0.084$). The mean social status of

mothers that produced twin litters sired by a single male was $+0.22 \pm 0.61$ ($n = 49$ litters), whereas that of mothers of multiple-paternity twin litters was -0.028 ± 0.62 ($n = 26$ litters).

Out of 24 observed copulations involving intromission and ejaculation, two or more males were present on eight occasions and in two cases females copulated with two different males in succession. Following the 24 copulations, 17 litters were observed, out of which eight survived until they could be genetically sampled. In all eight litters, paternity was allocated to clan males other than the male observed copulating. There were two mixed paternity litters, thus the mothers of these litters mated with at least three different males. Eleven females copulated between 9 and 45 days before conception and two females copulated 65 and 73 days, respectively, after conception, well into a pregnancy with a gestation of 110 days (Matthews 1939). Following all copulations, both partners intensively licked their genitals for many minutes.

(c) *Mate fidelity*

Out of the females with at least two litters (range of two to five litters, including 12 females with at least four litters) for which the sire was allocated with 95% confidence ($n = 52$), only 10 females produced more than one litter (two litters in all cases) sired by the same male. If we assume that, for the litters in this sample that were produced by a given female, the possible sires for each litter included all candidate males that were clan members on the date each litter was conceived, then it is possible to calculate the expected probability of any pair of litters having the same father under the assumption of random mate fidelity. Under this assumption, the overall probability of finding in the overall dataset at least one pair of litters with the same father was 0.759. The observed 11 pairs of litters with the same father, with a p of 0.069, are above the α of 0.05 that would allow the rejection of the null hypothesis of random mate fidelity.

(d) *Male manipulation*

The 62 males that 'shadowed' females successfully sired offspring with a mean of 2.8 ± 2.0 females in total, but shadowed on average 7.0 ± 3.5 females during their tenure (Wilcoxon test: $z = 6.189$, $p < 0.000\,01$) and sired cubs with only 1.2 ± 1.6 shadowed females (17.1%). Considering shadowing males that sired offspring, we tallied the number of females with whom they sired offspring and classified females as either shadowed or not shadowed by the male. Males gained paternity as often with females that they shadowed as with females that they did not shadow (Wilcoxon test: $z = 0.858$, $n = 27$, n.s.).

Out of 43 cases where a male 'defended' a female, in only three cases was the female within two weeks of the back-estimated time of conception and in all three cases the defending male was not the sire of the litter.

Most cases (94.7%, 36/38) of low-level harassment occurred between one and seven months before the female conceived, and in only two cases was the female within a two-week period of conception. In both of these cases the harassing male did not sire the litter. Out of 65 baitings, high-ranking females were baited more often ($n = 35$) than either mid- ($n = 16$) or low-ranking ($n = 14$) females ($\chi^2 = 2.4$, d.f. = 2, $p = 0.002$), suggesting that males

mostly attempted to manipulate the mate choice of high-quality females.

In 35% of baitings, the harassed female counter-attacked the group of baiting males with the assistance of other clan members. Only three baiting incidences occurred within two weeks of conception and out of these three litters the only genetically sampled litter was not sired by any of the males that baited the female. Two females were baited after conception.

Between 1987 and 2001 we observed two separate incidences when immigrants in two different clans attempted to kill cubs. In the first case, a male grabbed a seven-month-old cub of a mid-ranking female by the head when it was lying outside the den entrance. The cries of the cub caused several females to chase the male away from the den. The male dropped the cub and retreated. In the second case, a male spent half an hour attempting to dig out two one-month-old cubs of a high-ranking female that were inside a den hole before the mother returned and chased him away from the den.

(e) *Inbreeding*

Inbreeding between non-dispersing natal males and their sisters or mothers did not occur. Inbreeding between daughters and fathers was recorded in 0.8% of cubs (2 out of 236 cubs).

4. DISCUSSION

While our results and the subsequent discussion focus on the reproductive outcomes of male and female mating tactics, we note that the observed assortative mating pattern with respect to female age and male reproductive tenure (figure 4) has at least one other effect: it makes it unlikely that daughters mate with their fathers. The observed low level of inbreeding may also result from females recognizing fathers and other close relatives as kin and thus rejecting them as mates.

(a) *Male manipulation*

Our results indicate that males that 'shadowed', 'defended' and harassed females rarely gained the immediate benefit of paternity, and high-ranking males did not monopolize the paternity of offspring of high-ranking females, or indeed the offspring of mid- or low-ranking females (figure 2). We therefore found little evidence that these tactics provided males with a strong selective advantage, suggesting that females effectively countered these male tactics (see also § 4b). We also found no evidence that 'shadowing' strongly influenced female preference for males in the long term. Old females were more receptive to long-tenured males, and young females were more receptive to shorter tenured males, as predicted by patterns of affiliative male–female behaviour (East & Hofer 2001). This supports the idea that fostering relationships with females is a more successful male tactic than coercion or attempted monopolization (East & Hofer 1991; East *et al.* 1993). Thus, by displaying amicable gestures towards specific females, males may increase their chance of mating with these females. The fostering of amicable relationships with females and the formation of coalitions with females (East & Hofer 2001) may also help males

(particularly those of high rank) to stabilize their position in the social hierarchy.

(b) *Female counter-tactics*

Multiple mating was an important component of the reproductive tactics of Serengeti females. Our estimated level of polyandry is conservative, as some single-paternity twin litters might still be the product of sperm competition or cryptic female choice. If the two males have an equal chance then we will see only 50% of the mating polyandry revealed genetically, so 35% multiple paternity implies at least 70% multiple mating. This may be a minimal estimate because anything that makes the competition unequal will predict higher mating polyandry (Gomendio *et al.* 1998).

A relatively high proportion of mixed paternity would undermine attempts by dominant males to monopolize paternity. Kokko & Johnstone (1999) predicted that queues may be stable if paternity is not monopolized by high-ranking males. Our results confirm this prediction, and suggest that in addition to female behavioural interference (East & Hofer 2001) female mating tactics contribute to the stability of the male social queue.

We observed two failed attempts at male infanticide. Mating with multiple males may be a female tactic to reduce the incidence of male infanticide (Gomendio *et al.* 1998; Jennions & Petrie 2000), and observed copulations by hyena females that were unlikely to be receptive and those that occurred after conception also suggest that females may be attempting to confuse paternity in order to reduce infanticide (Hrdy 1977, 2000; Heistermann *et al.* 2001).

The observed low level of mate fidelity, while consistent with a model of random mate fidelity, does not imply that females mated randomly (cf. the assortative mating pattern with respect to tenure), merely that they apparently do not form serially monogamous relationships. It may suggest that there are several males within large Serengeti clans that offer similar fitness benefits to particular females (Johnstone *et al.* 1996) and that the choice of males in successive oestrus periods may vary because some males are absent while foraging on distant prey herds (Hofer & East 1993*b*). The combined effect of low mate fidelity and mixed paternity prevents male monopolization of paternity and decreases selection for physical contests for mates.

Although high-ranking females have the best opportunities to mate multiply, they employed this tactic significantly less often than did subordinate females, indicating that the benefit to dominant females of copulating with multiple males may be small in relation to the costs. Given the penile structure of the female clitoris, and the fact that females extensively clean their genitalia after every copulation, sexual transmission of infections may be a cost of multiple mating in hyenas. Owing to competition among males for access to high-ranking females, dominant females may rarely need to accept males of lower quality or spend much effort finding a high-quality mate, and thus the genetic benefits of multiple copulations may be marginal to them. Because low-ranking Serengeti females forage more often on distant migratory herds and return less often to the clan territory than do dominant females (East & Hofer 1991; Hofer & East 2003), their costs of mate choice will be comparatively high and thus they may

accept lower-quality males more often than would dominant females. Eight probable cases of mixed paternity were identified among 27 twin litters produced by females of unknown rank in a more strictly territorial clan (Engh *et al.* 2002), demonstrating that polyandry is not restricted to Serengeti hyenas.

Owing to the fission–fusion nature of clans, the lack of a breeding season and the commuting system of Serengeti hyenas, males may not always accurately track the reproductive states of all clan females, and this may explain why males 'defended', harassed and copulated with females that were unlikely to be close to ovulation. Females respond aggressively to certain males while tolerating others (East & Hofer 2001). Female aggression towards males is likely to be beneficial to females if it reduces the female costs of mate choice by hampering the attempts of unwanted males to assess the female reproductive state. As male hyenas do not feed offspring, females should prefer males that will increase the genetic quality and relative fitness of their offspring. Old age may be a reliable indicator of high male quality (Manning 1985; Kokko & Lindström 1996), and, as Serengeti females rarely mated with immigrant males with tenures of less than 2 years (figure 3) and female preference increased with male tenure (figures 3 and 4), females may use tenure as an index of male quality.

As recent immigrants are rarely selected as mates by Serengeti females, or by females in a Kenyan clan (Engh *et al.* 2002), female preferences may cause young males to delay full reproductive activity until many months after immigration. This idea is supported by the fact that testosterone levels of recent immigrants are low and similar to levels in natal males before dispersal, and testosterone levels of most immigrants increase only about 15 months after immigration (Holekamp & Smale 1998; Goymann *et al.* 2001, 2003).

Male fertility may decline with age (Trivers 1972; Hansen & Price 1995), and a lack of paternity at the end of the tenures of Serengeti high-ranking males may indicate a deterioration in sperm production or sperm viability when males reach extreme old age. If some males have low fertility, females could compensate by mating multiply.

Engh *et al.* (2002) concluded that a rate of reproduction for alpha males lower than that of their beta males in a Kenyan clan supported a 'limited control' model of reproductive skew. We suggest that low fertility among elderly alpha males is an alternative explanation for the reduced success of their alpha males.

The lack of a strong preference among Serengeti females for a few male clan members indicates that there is not a limited number of 'high-quality' males, but suggests that genetic compatibility (Zeh & Zeh 1997) may be a more significant component of female mate choice. Females in various mammalian species choose males with major histocompatibility complex (MHC) haplotypes that differ from their own (Potts *et al.* 1991; Wedekind & Füri 1997). As MHC is associated with body odour, male odour may be an important trait that influences female mate choice.

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