Male spotted hyenas (*Crocuta crocuta*) queue for status in social groups dominated by females

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A long-term study of immigrant male spotted hyenas (*Crocuta crocuta*) living in large multimale/multifemale groups (clans) demonstrated that males acquire social status by queuing. Maximum likelihood estimates of parameters of a stochastic queuing model that assessed queuing discipline confirmed that immigrant males respected the convention that their positions in a queue of typically 15 or more individuals was determined by their sequence of arrival. Levels of aggression among males were low; males did not attempt to improve their social status through physical contests. Size and body mass did not influence male social status. The stability of queues was insured by an increase in the rate at which males formed coalitions against other males as they rose in social status and by coalitions between high-ranked males and dominant females. High-ranked, long-tenured males chiefly consorted with (''shadowed'') and focused their affiliative behavior on females of high reproductive value and disrupted attempts by subordinate males to associate with these females. High-ranked males also supported females against lower-ranked males that harassed them. In contrast, lower-ranked, short-tenured males focused their affiliative behavior on young adult females and rarely shadowed or defended females. Males that did not disperse from their natal clan (nondispersers) quickly acquired top rank in the male social hierarchy. Irrespective of the social status acquired from their mother when young, nondisperser adult males submitted to all adult females. *Key words:* aggression, *Crocuta crocuta,* queuing, social status, spotted hyenas. *[Behav Ecol 12:558–568 (2001)]*

Competition among males for access to mates can be intense and can result in high variance in male reproductive success, particularly in polygynous species. Sexual selection favors male traits that are attractive to females and that increase competitive ability. For example, costly sexual advertisement (Borgia, 1985; Hamilton and Zuk, 1982; Zahavi, 1975) and symmetry in body characters (Møller and Höglund, 1991) have been viewed as signals of male quality. Large males prevent physically inferior males from gaining access to females (Clutton-Brock, 1989; Emlen and Oring, 1977) and reduce the cost incurred by females due to harassment by marginal males (Cassini, 1999; Clutton-Brock et al., 1993; Modig, 1996; Nefdt, 1995; Poole 1989; Wikelski et al., 1996). Small males use different tactics that utilize their greater agility (Arak, 1988; Steele and Partridge, 1988). Older males may be better able to provide resources for their offspring and mates (Côté and Hunte, 1993; Kokko, 1997), and old age may be an indicator of viability (Kokko and Lindström, 1996).

In a variety of species, males queue or ''stand in line'' to gain access to mates. Male thirteen-lined ground squirrels (*Spermophilus tridecemlineatus*) form queues of short duration (Schwagmeyer and Parker, 1987), and much longer-term queues have been described in many cooperative breeding species (Wiley and Rabenold, 1984), in oystercatchers (*Haematospus ostralegu*; Ens et al., 1995), and in several lekking species of birds, such as long-tailed manakins (*Chiroxiphia linearis*; McDonald, 1989) and black grouse (*Tetrao tetrix*; Kokko et al., 1998).

Queues may operate according to a strict convention in that access to mates is determined by the sequence in which males join queues. Alternatively, movement to the head of a queue may be influenced by both the sequence in which individuals joined the queue and the characteristics of queuing individuals (Kokko et al., 1998). Unlike conventional contests where there are winners and losers (Maynard Smith, 1982), queuing males that survive for a sufficiently long period can eventually expect to gain access to mates. Differences in survivorship, however, will influence the reproductive success of males that have to queue for long periods before acquiring mates. Late arrivals to queues might be expected to try to ''jump the queue'' if they are likely to gain more immediate access to females by such action. If queue jumpers frequently obtain mates before males that respect queuing conventions, then queuing would not be an evolutionarily stable convention (Schwagmeyer and Parker, 1987). Maynard Smith (1983) suggested that queues are likely to be stable if the value of the contested resource was low in relation to the cost of violating the queuing convention and if early arrivals in the queue have a greater resource holding potential (RHP) than late arrivals. He also suggested that in human queues cooperation between waiting individuals could provide stability.

We have proposed that in large, stable social groups of spotted hyenas (*Crocuta crocuta*), immigrant males queue for social status in a linear dominance hierarchy, and while doing so they cultivate relationships with the more dominant female members of the group (East and Hofer, 1991). Close relationships with females are essential because of the unusual reproductive anatomy of females (East et al., 1993). Female spotted hyenas have a peniform clitoris that is positioned between their hind legs, with the opening to the reproductive tract at the tip of the clitoris that points forward. Although the peniform clitoris is not erected during copulation (East et al., 1993), its position and structure ensures that males can only copulate successfully with the complete cooperation of the female (East et al., 1993; Kruuk, 1972). To secure such co-

operation, males need to develop close relationships with females over a period of time (East and Hofer, 1991; East et al., 1993; Hofer and East, 1995b). In this respect, males with long tenure have an advantage over more recent immigrants because of their longer term relationships with females. We have argued that aggression among queuing males is low because a close relationship with a female is a nontransferable resource and cannot be acquired through physical contests (East and Hofer, 1991; East et al., 1993). Thus, we consider that female control over mating in spotted hyenas has favored the submission of males to females and the lack of selection for physical contests among males (East et al., 1993; Hofer and East, 1995b).

In this study we used long-term data from individually known spotted hyenas from three social groups in the Serengeti National Park, Tanzania, to demonstrate that male social status is linked to tenure and is not influenced by phenotypic traits such as body size. We applied a stochastic queuing model to establish that males acquire social status by queuing. We then considered factors that contribute to the stability of the male social queue. We propose that the most important resource that immigrant males acquire by queuing is mating opportunities, and we predict that immigrant males with high social status should be better able to compete for access to females than males of lower social status.

Queue jumping should be most strongly discouraged by males that have invested most time in queuing and those that stand to lose benefits associated with high status. Thus, we predict that males with high rank and long tenure should enforce queuing conventions more vigorously than low-ranked, recent immigrants. As cooperation among queuing males is likely to be more effective in preventing queue jumping than the actions of individuals (Maynard Smith, 1983), we predict that male coalitions may play a role in the stability of the male social queue. If so, high-ranked males should form coalitions against other males more often than more subordinate males, and individual males should not attempt to jump the queue. However, coalitions of queue jumpers may succeed if they challenge an individual or smaller coalition ahead of them in the queue.

If females are more likely to mate with males that have developed long-term relationships with them, then we would expect males and females that have associated for long periods of time to have stronger relationships than those that have associated for short periods. We also predict that short-tenured males should seek to diminish this asymmetry by developing relationships with young females that have short reproductive associations with all males. By primarily developing relationships with older females, males with long-term tenure would avoid inbreeding with their female offspring.

METHODS

Study population

In the Serengeti National Park, Tanzania, spotted hyenas live in large, stable social groups or clans that contain approximately the same number of adult males and females (Hofer and East, 1993a, 1995a). Data used in this study were obtained from three clans that were studied for approximately 12 years (May 1987–June 1999), 9 years (November 1989–June 1999), and 8 years (August 1990–June 1999), respectively. Clan members were individually known (Hofer and East, 1993a, 1995a). Females remain in their natal clan, and all adult females breed (Hofer and East, 1993c). During the study period, a total of 60, 59, and 61 adult females were observed in the three study clans, respectively. Females were aged on the basis of their known birth dates. Previously it has been reported that male spotted hyenas disperse from their natal group, and breeding males in a clan are immigrant males (Frank, 1986; Kruuk, 1972; Mills, 1990). The average annual rate of mortality for immigrant males was 15.6% (Hofer et al., 1993). During the study period, a total of 42, 42 and 41 immigrant males were observed in the three study clans, respectively. In addition, one natal male from each of two study clans and two natal males from the third clan did not disperse and became part of the male dominance hierarchy in their natal clan. We refer to natal males that did not disperse as ''nondispersers.'' When discussing both immigrant males and nondisperser natal males, we refer to ''postdispersal'' males. Behavioral data from ''predispersal'' males that operate within the social system of their natal clan as offspring of their mother were not included in this study.

Social status

We determined social status of males chiefly from submissive acts (retreat, displacement, cower, tail between legs, ears back, head bobbing, head upside down) and occasionally from aggressive acts (direct approach, push, stand over, lunge, chase, bite) in dyadic interactions recorded ad libitum and during focal observations of individuals. The death or disappearance of males and the immigration of males altered the male dominance hierarchy. When such changes occurred, we determined a new rank for all postdispersal male clan members from dyadic interactions.

Postdispersal males and adult females were assigned a standardized rank for comparison of ranks across clans. This measure distributed ranks evenly between the highest rank (standardized rank $+1$) and the lowest rank (standardized rank -1), with the median rank being scored as 0. Individuals with standardized ranks within the top, middle, and lower third of the total range of values were then classified as high-, mid-, or low-ranked.

Body size parameters

We compared body size parameters from 10 immigrant males with the rate at which these males increased in social status. Body size parameters were obtained from anesthetized animals following the procedure described by Hofer and East (1993a). Body length was measured from the back of the skull to the tail root and thus excluded head and tail length. Because spotted hyenas have the ability to consume large amounts of food, body mass can be influenced by the amount of food in the digestive system (Kruuk, 1972). For this reason, measures of body mass used in this study were only from males with ''normal'' belly scores. We calculated the rate at which males increased in status by dividing the number of rank positions by which they advanced in status by the duration of the period between the date of the first status increase to the date on which the highest lifetime status was acquired.

Male tenure

We calculated the total tenure of an immigrant male as the period between the date on which the male was first observed in the new clan territory and the date of the last sighting or death of the male. Tenures of males were also calculated for particular events as the period from the date on which the male was first observed in the clan territory until the date of the event in question. When the position of males in a social queue changed due to death, disappearance, or immigration of another male, we recalculated the tenure and social status of males in the queue. A minimum (censored) period of tenure was calculated for immigrant males that were already es-

tablished in a clan when the study commenced and for those that joined a clan during the study and were alive when the study ended. The tenure of males that remained in their natal clan to breed was calculated to begin at the age at which males attained adulthood (2 years of age).

To investigate whether the tenure of a male influenced his behavior toward adult females of different age, we classified the behavior of males that approached to within 5 m of a female as "affiliative" if he greeted (East et al., 1993) the female, groomed the female, or rubbed his body or head against that of the female, or "other" if the male approached the female without displaying affiliative behavior. Males were categorized as those with no more than 3 years tenure and those with tenure longer than 3 years. Adult females were divided into two age classes, those no more than 5 years of age (i.e., females within 3 years of reaching adulthood), and those older than 5 years of age. The former group consisted mainly of first-time breeders; the latter consisted mainly of experienced breeders. Male–female interaction data were obtained from focal samples of males observed chiefly at the clan communal den or recorded ad libitum during encounters between males and females. The mean duration of 151 focal samples from 57 males was 41 ± 38 min. To avoid pseudoreplication in behavioral data, we included only one interaction by a specific male with a specific female in analyses of behavioral data. If more than one interaction between a particular male–female combination occurred in the behavioral data, then a single interaction was selected at random.

We used the same categories of females and males to examine the response of young and older females to the approach of shorter or longer tenured males. The response of females to males were defined as (1) directly aggressive if the female chased or bit the male, (2) threatening if the female glared, got to her feet, approached with her tail raised, pushed or lunged without making contact with the male, or (3) other, which were chiefly neutral responses in which the female did not react to the male or (rarely) affiliative responses (grooming, greeting).

Coalitions

Immigrant males were considered to have formed a coalition with other postdispersal males or adult female clan members if they joined an on-going conflict by siding with one of the opponents. In addition, they participated in display coalitions in which two or more animals "walk parallel" (Kruuk, 1972) without directing this display toward another clan member. When parallel walking, one or both partners often raised their tails, groaned, and investigated scent marks. Display coalitions may signal an intention to cooperate with other members of the coalition and advertise the existence of the coalition to other group members. Male coalitions mostly involved coalition partners walking or running toward the target male that then retreated. Male coalitions that challenged females, a behavior termed "female baiting" (Kruuk, 1972), involved males approaching a female with an aggressive posture and occasionally biting the female.

Shadowing

Frank (1986: 1520) stated that courtship in spotted hyenas consists of two levels of attendance behavior:

> The first is "following," the male trailing behind a walking female, stopping when she does and lying near her when she enters a day bed. The second is "consortship," the same male being seen with a given female on two or more consecutive sightings of the female. Eventually, one

or more males form a more lasting association, attending her closely for days or weeks, the highest ranking male staying closest to her and occasionally threatening others that approach her too closely.

We have not applied these definitions because we consider following behavior and consortship to be essentially the same behavior. Instead, we apply the term "shadowing" (East and Hofer, 1991) for males that actively follow a female, regardless of how many days the male follows the female. Some shadowing males excluded more subordinate males from close proximity (0–20 m) of the female they followed, and males that were not shadowing also excluded subordinate males from close proximity with particular females or groups of females. Exclusion was typically achieved by low-level approach and displacement interactions. By excluding subordinate males from females, dominant males defended their priority of access to females and disrupted attempts by other males to develop relationships with females.

We recorded the identities of the male(s) and female involved in shadowing associations when this behavior was observed. Only one record per day for a specific shadowing association was included in the analysis. The rate at which a male shadowed females was calculated by dividing the total number of shadowing cases for each male by his tenure in the clan. Only males with tenure of at least 6 months were included in the analysis. We calculated the rate at which each female was shadowed by dividing the number of instances she was shadowed by her tenure as an adult clan member. Females were considered independent and adult at 2 years of age; all have their first estrous cycle and most give birth during the 2 years following independence. Calculation of the rate at which females were shadowed was thus restricted to females that were observed for at least 2 years after independence.

Estrus and conception dates

To assess whether shadowing was linked to estrus, we required an estimate of the likely estrous period for females. For females that were shadowed, we calculated the conception date of their litters from the birth date of the litter, based on a 110-day gestation period (Matthews, 1939). Birth dates for litters were either known or estimated from the pelage and locomotory abilities of cubs and are likely to be accurate ± 7 days (Hofer and East, 1993c). Schneider (1952) quoted an estrous period of 1 day. As it is possible that estrus may last for several days, we estimated two periods during which estrus was likely to occur; one spanning a period of 7 days before and after the estimated conception date, and another spanning 15 days before and after the estimated conception date.

Queuing discipline

We assessed the degree to which males observed the queuing convention (queuing discipline) in a number of ways. First, for all immigrant males with at least six changes in social status, Wilcoxon signed-rank tests were used to investigate whether successive changes in rank position for each male involved an increase in social status. Rank changes due to nondispersing natal males joining the male dominance hierarchy were excluded. Second, for each clan we calculated maximum likelihood estimates for a quantitative measure of queuing discipline, a pair of indices introduced in a stochastic queuing model by Kokko et al. (1998). Kokko et al. (1998) distinguished two processes that affect the position within a queue: the integration of newcomers, represented by the newcomer priority index, P, and the strictness by which established males adhere to the queuing convention, reflected by the rank pri-
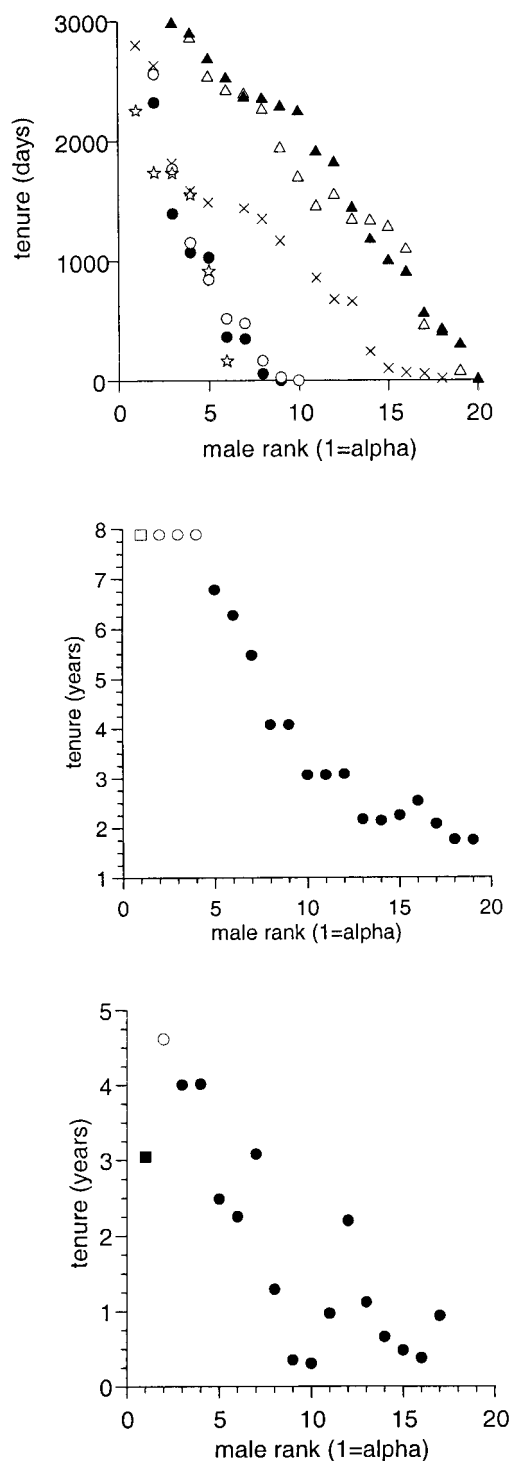
Figure 1
Upper panel, the changes in social status in relation to tenure for two males from each of three study clans. Mamba clan (M42, filled triangles; M189, open triangles), Pool clan (P31, filled circles; P50, open circles), Isiaka clan (I108, crosses; I189, stars). Center panel, a dominance hierarchy, or male queue, in the Mamba clan after the death of the alpha male and the move of the beta male (a natal male represented as an open square) to the alpha position. The filled circles represent immigrant males that joined the clan after the start of the study and thus have uncensored tenures. The open circles represent males that were already clan members at the beginning of this project, and thus have censored tenures. Lower panel, a dominance hierarchy, or male queue, in the Pool clan at the point in time when a natal male (represented as a filled square)

ority index, Q. Briefly, P describes the disadvantage of a new-comer to move to a position of high social status when trying to join a clan compared to the chances of the average established male already present in the hierarchy. At $P = 0$, no newcomer could bypass an established male in the hierarchy (i.e., the newcomer always joins at the bottom). At $P = 1$, the chances of newcomers and established males are equal, and if $P > 1$ newcomers would benefit from not having previously been a member of the queue. If $Q = 0$, then the current social status would be irrelevant for arranging the ranks among all males once the newcomers joined, whereas $Q = 1$ describes a strict and impartial "first in, first to the top" queuing convention. Thus, the null hypothesis of random order and lack of queuing discipline is equivalent to the pair of values (P, Q) = (1, 0), and the log-likelihood ratio test G can be used to test whether empirical estimates of (P, Q) for a given queue significantly deviate from the null hypothesis. Further details on how empirical estimates for (P, Q) are computed can be found in Kokko et al. (1998).

Statistics

Statistical and graphical analyses were performed using SYS-TAT 9.0 (Wilkinson, 1999). All statistical tests are two-tailed. Means are given ± SDs. Immigrant males that were members of study clans at the start of the study and immigrant males that were alive at the end of the study provided censored data on tenure. We calculated the significance of Spearman rank correlations according to Siegel (1956).

RESULTS

Male immigration

The age at which 14 known natal males joined a new clan was 4.12 ± 1.31 years. There was no significant effect of maternal rank on the age at immigration (Spearman rank correlation, $n = 13$, $\rho = 0.423$).

Tenure and rank

When males first immigrated into a clan, they were submissive to all clan members and thus acquired a dominance rank at the bottom of the social hierarchy. On five occasions, coalitions of immigrant males below median rank chased males that were in the process of immigrating into the clan for distances of at least 100 m. These long chases were unlike the interactions among established immigrant males that involved displacements by only a few meters. These observations suggest that males below median rank are more aggressive to new immigrants than to established immigrants, and this may ensure that new males join the bottom of the hierarchy.

During the study immigrant males died or disappeared, and new immigrants joined clans. Figure 1 plots the change in social status in relation to tenure for two males from each of the three study clans. These data show that immigrant males gradually increased in social status as their tenure increased and as those above them in the hierarchy died or disappeared. When immigrant males acquired a new rank, their social position altered by only one or two rank positions. Sudden, large

←

became alpha male. The filled circles represent immigrant males that joined the clan after the start of the study and thus have un-censored tenures; the open circle represents a male that was already a clan member at the beginning of the project and thus had a cen-sored tenure.

changes in social status were not observed among immigrant males. For all ($n = 68$) immigrant males with at least six changes in social status, the majority (78%, $n = 53$) showed that new ranks were significantly more likely to be of a higher status than the previous rank. Thus, more males than expected by chance increased their social status in a manner consistent with a strict queuing convention ($\chi^2 = 21.24$, df $= 1$, $p < .00001$). This was particularly true of immigrant males in the largest clan (Mamba), where the hierarchy consisted of at least 20 males at any point in time during the study. Here, 26 out of a total of 28 (93%) immigrant males showed a consistent, steady improvement in social status whenever their rank changed. In the two smaller clans (Pool and Isiaka) with between 10 and 15 immigrant male members at any one time, a smaller proportion of rank changes conformed to a strict queuing convention. In the Isiaka clan 13 (68.4%) of 19 males and in the Pool clan 14 (67%) of 21 showed a significant, consistent increase in social status. In the minority of cases when an immigrant male's social status declined, the mean rank change was small (1.2 ± 0.5 rank positions, $n = 47$ males). Such incidences mainly occurred when immigrant males had not been clan members for a long period (mean tenure 332 ± 61 days) and had low social status (highest social status of males suffering a decline in social status had a mean rank $= 12.0 \pm 5.7$, when the alpha male had a rank of 1).

The center panel in Figure 1 illustrates an example of a strict queue in the Mamba clan after the death of the top-ranked male and the advancement of the second-ranked male to the top rank. The lower panel in Figure 1 illustrates a less strict queue in the Pool clan.

During this study, 13 snapshots of male queues, like that plotted in the upper panel of Figure 1, could be taken after the acquisition of the alpha position by a male. Excluding individuals with censored data on tenure and nondisperser natal males, results from linear regressions indicate that the longer the male queue, the more years an immigrant male takes to reach the alpha position. In the large Mamba clan, males required between 7 and 8 years to become the alpha male, whereas in the smaller Pool and Isiaka clans males required between 4 and 5 years.

In contrast to immigrant males, nondisperser males that remained in their natal clans to breed did not follow the queuing convention and acquired a high rank in the male dominance hierarchy when they ceased to socially operate as an offspring of their mother and began to behave like an immigrant male (see below).

Queuing discipline

A quantitative measure of queuing discipline is provided by the newcomer priority index, P, and the rank priority parameter, Q. Maximum likelihood estimates for the parameter pair (P, Q) over the entire study period were the value pairs (0.01, 0.74) for the Isiaka clan, (0.01, 0.72) for the Mamba clan, and (0.01, 0.74) for the Pool clan. Each of the three pairs of values were highly significantly different ($p < .000001$) from the null model.

Male–female relationships

Does the length of an association between a male and female influence their behavior toward each other? Considering only one randomly chosen interaction by a specific male with a specific female, we found that long-tenured males (with more than 3 years tenure) were equally likely to show affiliative behavior to both young (18 affiliative acts in 127 approaches) and older females more than 5 years of age (6 affiliative acts in 67 approaches, $\chi^2 = 1.102$, df $= 1$, $p = .30$). In contrast,
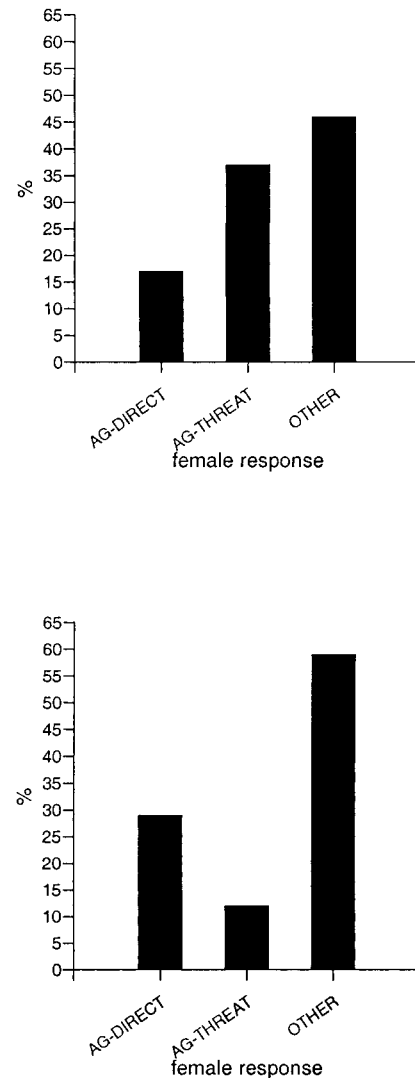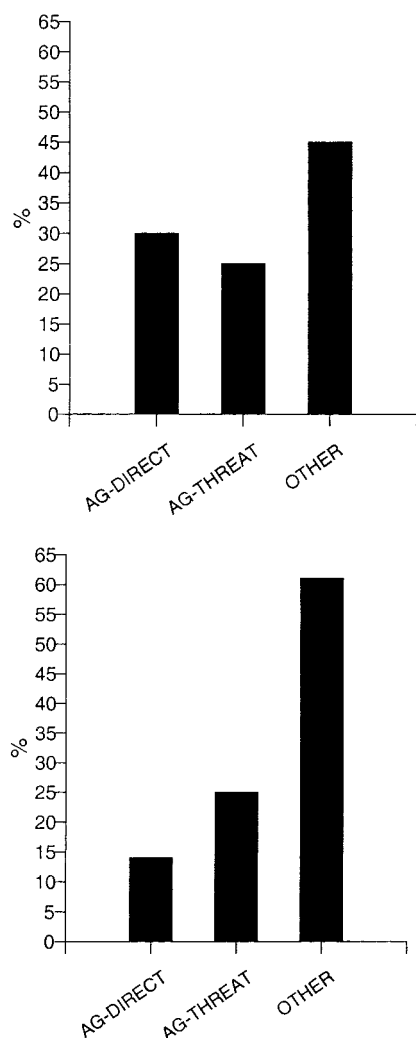

Figure 2
The response of young females (no more than 5 years of age) to the approach of males. Upper panel, the response to males with a short tenure of no more than 3 years. Lower panel, the response to males with a longer tenure of more than 3 years. AG-direct: an aggressive response involving chasing or biting; AG-threat: an aggressive response limited to threats; other: a response that was not aggressive.

short-tenured males (with no more than 3 years tenure) showed a higher incidence of affiliative behavior toward younger females no more than 5 years of age (5 affiliative acts in 40 approaches) than older females (0 affiliative acts in 62 approaches, $\chi^2 = 8.149$, df $= 1$, $p = .004$).

Does the length of their association influence the response of a female to the approach of a male? The response of young females to short-tenured males was different from their response to males with longer tenure ($\chi^2 = 9.975$, df $= 2$, $p = .007$; Figure 2). Young females were more frequently directly aggressive to approaches by long-tenured males than they were to more recent immigrants. In contrast, young females showed less direct aggression to short-tenured males, but frequently gave low-level threats to such males when they approached.

The response of older, experienced females to approaches by recent and longer tenured males also differed ($\chi^2 = 7.825$, df $= 2$, $p = .02$; Figure 3). Older females threatened both
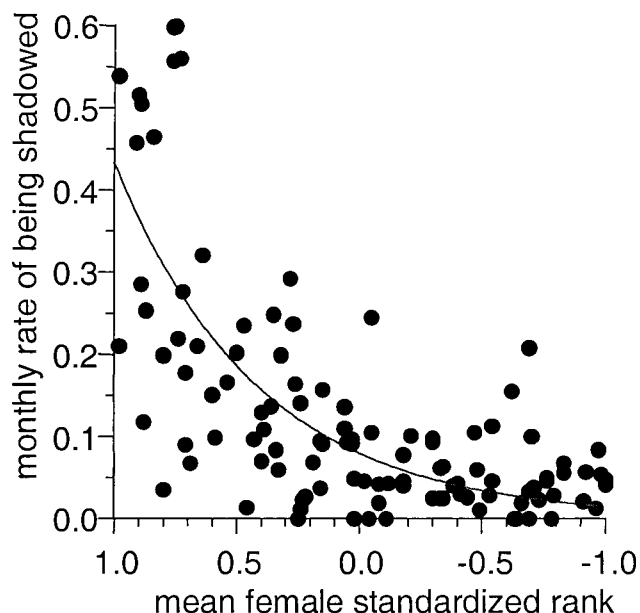
Figure 3
The response of older, experienced females (more than 5 years of age) to the approach of males. Upper panel, the response to males with a short tenure of no more than 3 years. Lower panel, the response to males with a longer tenure of more than 3 years. AG-direct: an aggressive response involving chasing or biting; AG-threat: an aggressive response limited to threats; other: a response that was not aggressive.

recent and longer tenured males; however, they were more frequently directly aggressive to shorter tenured males than to longer tenured males.

One case of a coalition of 10 females attacking a mid-ranked male was observed. The reason for the attack was unknown. The male was not observed for more than a month after the attack. He reappeared in the territory for a few days and then was not seen again. This incident demonstrated that females directly influence membership of the male queue.

Natal males

One hundred twenty-eight natal males from the three study clans survived beyond the age of 16 months and thus were potential dispersers (Hofer and East, 1995a). Of these, four natal males in three study clans did not disperse. These non-disperser males were sons of mid- and low-ranked females. They acquired alpha status within a period of months after they ceased to operate as the offspring of their mothers and started to behave toward adult females in a manner similar to

Figure 4
The rate at which females were shadowed in relation to their mean standardized rank (rank 1 is top rank). $\rho = 0.637$, $n = 111$ females, $p < .0001$. The fitted equation is: $y = 0.080*e^{-1.690x}$, $r^2 = .530$.

that of immigrant males (Figure 1). They were then able to exclude all immigrant males from close proximity with females they defended. Nondisperser natal males habitually submitted to all females, including females that they dominated when young and associated with their mother's social status.

Body size and social status

The rate at which males increased in social status was not correlated with their body mass ($\rho = 0.575$, $n = 8$), body length ($\rho = 0.050$, $n = 9$), chest girth ($\rho = 0.485$, $n = 10$), or shoulder height ($\rho = -0.250$, $n = 10$).

Shadowing

Immigrant males rarely shadowed females when they first joined a clan. The mean interval between immigration and the first case of shadowing behavior was 1.6 ± 1.0 years ($n = 64$ males). Females were shadowed mostly by a solitary male (92%, $n = 994$), occasionally by two males (7%), and rarely (1%) by larger groups of three to eight males. High-ranked females were shadowed at a higher rate than lower-ranked females (Figure 4) and some mid- and low-ranked females were rarely if ever shadowed by males.

The rate at which high-ranked males shadowed females was higher than that of lower-ranked males, and some males were rarely if ever observed shadowing females (Figure 5). High-ranked males shadowed a larger number of individual females than lower-ranked males (Figure 6), but they did not shadow all female clan members. Instead, shadowing effort was focused on a few specific females. For example, the male in each study clan that held the alpha position for the longest periods (censored tenures of 5.3, 7.0, and 9.0 years, respectively) only shadowed 10 of 37, 10 of 52, and 8 of 61 of available females, respectively, during the years they were alpha males. All three alpha males focused their shadowing effort on a few high-ranked females (75% of shadowing effort on two females, 69% on three females, and 70% on two females, respectively).

The duration of shadowing associations varied (range 1–119
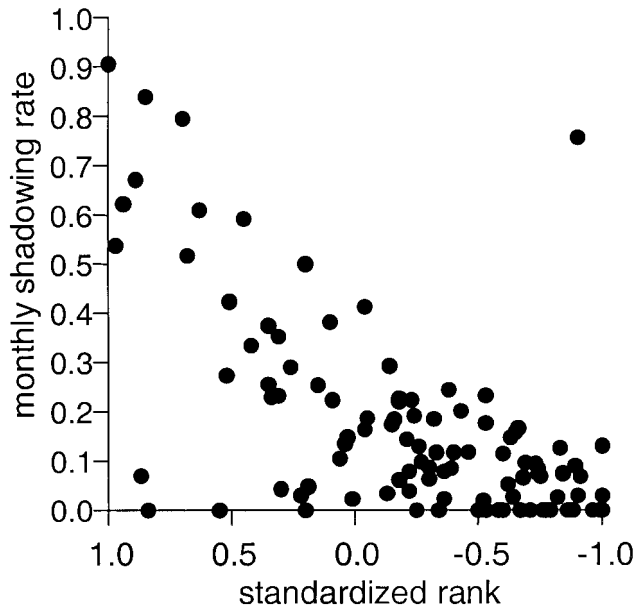
Figure 5
Male monthly shadowing rates in relation to mean standardized rank (rank 1 is the top rank). $\rho = 0.563$, $n = 101$ males, $p < .0001$.

days), with most associations (89%) persisting 1–3 days and only rarely (11% of 806 associations) for longer periods. Only 11 of 105 males shadowed a specific female for 14 days or more (14–43 days); 5 of these were alpha males and all 11 males were above median rank. In one case a nondisperser natal alpha male shadowed a female for 119 days.

Of 1171 shadowing associations for which the conception date for a female's next litter was known, only 5% occurred within the 2-week period spanning the calculated conception date, and only 10% occurred within the month spanning the calculated conception data (15 days before and 15 days after the conception date). These results indicate that males frequently shadowed females that were not in estrus.

In the Serengeti, spotted hyenas regularly commute to feed on migratory herbivores up to 70 km from their territory (Hofer and East, 1993a,b). Males were observed following commuting females when they departed from or returned to their territory. Males that shadowed particular females inside their territory were relocated within days in association with the same female long distances away from the territory. These observations indicate that males shadow females even when they commute.

Defense of females

Males that shadowed females and males associating with females in the vicinity of the den or at resting sites prevented lower-ranked males from approaching the females. Exclusion was mostly achieved by approach-and-retreat interactions. Figure 7 shows that males below median rank rarely defended females in this way, but males above median rank frequently did so and mostly defended females that were above median rank. Considering those males observed interacting with females, we compared the number of males recorded defending females (22 males above and 0 males below median rank) with those that were never seen defending females (19 males above and 42 below median rank) and found that males below median rank never defended females, while those above median rank frequently did so ($\chi^2 = 30.665$, df $= 1$, $p < .000001$).

Males with short tenure rarely attempted to defend females,
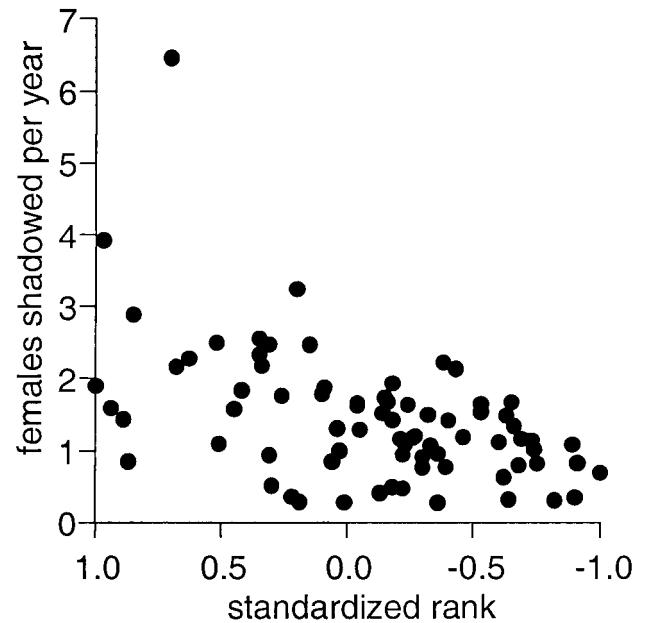
Figure 6
The number of females shadowed per year in relation to mean standardized rank (rank 1 is the top rank). $\rho = 0.481$, $n = 76$ males, $p < .002$.

but when they did so, they defended young females that had recently become adults (Figure 8). Males with longer tenure chiefly defended adult females with longer tenure (Figure 8).

Coalitions among males

We predicted that high-ranked, long-tenured males should form coalitions more often than lower ranked males. For the following analysis, we used data from all males that progressed
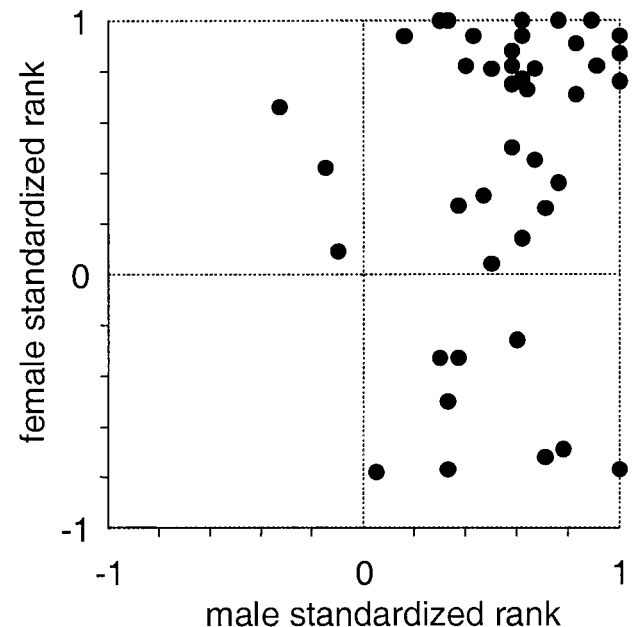
Figure 7
The standardized rank of females that were defended in relation to the standardized rank of the defending male (rank 1 is top rank). $\rho = 0.305$, $n = 54$ male–female pairs, $p < .02$.
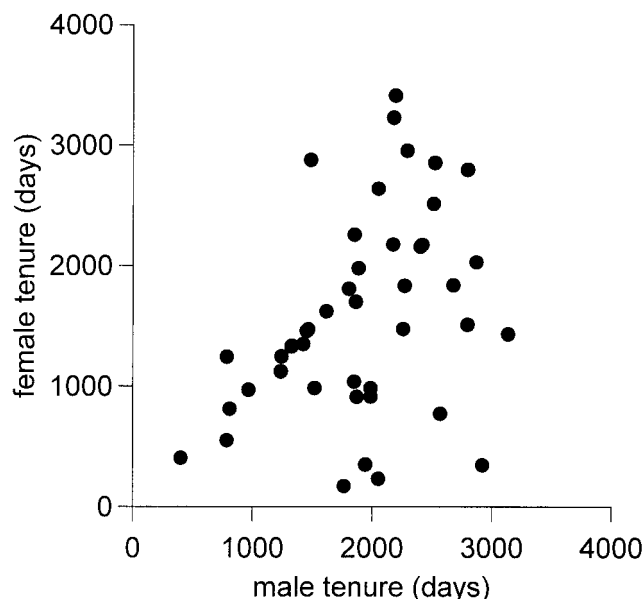
Figure 8
The tenure of females in relation to length of tenure of males that defended them. $\rho = 0.413$, $n = 54$ male–female pairs, $p < .005$.

from low to middle status and ultimately obtained high social status during the study ($n = 30$ males). For each male we calculated the rate at which he joined coalitions during the period he held low, middle, or high rank. Monthly rates at which males participated in coalitions against other males increased as they rose in rank from low through middle to high status (Friedman ANOVA $= 6.067$, df $= 2$, $p = .048$).

Despite long-term observations of three clans for 8, 9, and 12 years, we observed only one incidence of severe aggression among males. This involved a coalition of two immigrant males (ranked 4 and 7) briefly attacking another immigrant male ranked 3 and inflicting deep wounds. The tenures of the males ranked 3, 4, and 7 on the day of the attack were 3.5 years, 2.9 years, and 2.7 years, respectively.

Coalitions between males and females

Coalitions between postdispersal males and adult female hyenas were rare. Of a total of 129 postdispersal males, only 19 males, all high-ranked (mean standardized rank 0.8 ± 0.2) were observed in 27 coalitions with females. The targets of male–female coalitions were always males with a lower rank than the supporting male. Males chiefly formed coalitions with high (59%) and mid-ranked (30%) females. We found no evidence that low-ranked males attempted to increase their social status by forming coalitions with females when these females challenged higher-ranked males.

Harassment of females

Although females are dominant to males, males harass females. Single males harass single females by stalking them or approaching them in an aggressive manner, then lunging and occasionally biting them on their legs or rump. Of 501 interactions with females that involved a single male, 6% involved this form of harassment. Most of this harassment was from mid-ranked males (55%). Harassment by low-ranked (24%) or high-ranked males was less common (21%). Females that were bitten by males on their legs often limped for several days, which may have impeded their ability to hunt.

Groups (two to seven individuals) of males occasionally ag-

gressively harassed or "baited" females. Of 348 male coalitions, 28% were formed to bait females. When baited, females were often supported by other females, and on seven occasions they were supported by high-ranked males.

DISCUSSION

This long-term study demonstrated that the social status of immigrant male spotted hyenas increased with their length of tenure in a clan (Figure 1). Physical contests were not used to improve social status, and the rate at which males increased in rank was not related to body mass or body size. The hierarchy among immigrant males can be described as a social queue, and we have shown that hyena males observe strict queuing conventions. A benefit linked to high male social status was increased access to female clan members (Figures 5 and 7).

Male social queues

Immigrant males observed a queuing convention whereby successively arriving individuals waited their turn to rise in social status, and males did not use aggressive contests to improve their status. Both quantitative measures of queuing discipline introduced by Kokko et al. (1998), the newcomer priority index (P) and the rank priority index (Q), confirm this. The low value of P (0.01) for all three study clans implies that males almost always join at the bottom of the hierarchy, and this value was substantially lower than that (0.28) reported for queues of a similar length at black grouse leks (Kokko et al., 1998). The values of Q of between 0.72 and 0.74 were substantially higher than the overall value for black grouse of 0.53 and indicated that male spotted hyenas show a far more strict queuing discipline than black grouse. We found no evidence that phenotypic characteristics such as skeletal size (body length, chest girth, shoulder height) or body mass influenced the rate at which males progress along the queue.

Queue stability

In the thirteen-lined ground squirrel, queuing conventions collapse when more than two males form a queue (Schwagmeyer and Parker, 1987). In contrast, queues that involved numerous male spotted hyenas were stable throughout this long-term study, and males in queues of more than 20 animals observed queuing conventions (Figure 1).

Maynard Smith (1983) suggested that queues may be stable if the value of the contested resource is low in relation to the cost of violating the queuing convention. We showed that experienced breeding females are more tolerant of high-ranked males with longer tenure than they are of recent immigrants. This suggests that if short-tenured males attempt to mate with such females, they are likely to be aggressively rejected, and thus such females are of low value to them.

It has been argued that queues may be stable if early arrivals in queues have a greater resource holding potential (RHP) than later arrivals (Maynard Smith, 1983). Because the rate of status increase by males is not related to measures of body size or mass, RHP does not appear to be a simple phenotypic property. We found that when males achieved high status, they formed coalitions with other queuing males more often than when they were mid- or low-ranked. Our results therefore suggest that coalitions among high-ranked males may increase the RHP of early arrivals. The importance of such cooperation was acknowledged by Maynard Smith (1983) in his discussion of the stability of human queues.

High-ranked males supported adult females that challenged lower-ranked males. High-ranked males also supported fe-

males that were harassed or baited by groups of lower-ranked males. Coalitions with socially dominant females probably reinforce the stability of the male hierarchy and may also strengthen bonds between high-ranked males and females.

One successful case of aggressive queue jumping was observed that involved a coalition of two immigrant males. The asymmetry in tenure and rank between the attacking coalition and victim was modest, and the victim was successfully evicted from the male queue. This observation suggests that male coalitions may be more effective than individuals in successfully jumping the queue, but coalitions are rarely formed to achieve this rise in status.

Greeting ceremonies are used by spotted hyenas to signal acceptance of their social status to more dominant individuals. As greetings among immigrant males chiefly involve individuals of similar social status (East et al., 1993), greeting ceremonies probably confirm relative status between males of adjacent rank and, by doing so, may help to maintain the stability of queues.

Male–female behavior

Shadowing was not restricted to the estrous period of the female, so this behavior may help males to strengthen relationships with females. If so, high-ranked males invested more in fostering relationships with females than did more subordinate males (Figures 5 and 6), and top-ranked males focused their shadowing effort on a few high-ranked females.

Long-tenured males displayed more affiliative behavior to older than to younger females, and older females responded with less direct aggression to long-tenured than to short-tenured males. These results suggest that long-tenured males seek mating opportunities with older females with breeding experience and that young females are less desirable mating partners. This may be because first-time breeders are more likely than experienced breeders to produce no surviving cub or a surviving singleton rather than a twin litter (Hofer H and East ML, unpublished data). High-ranked females are also valuable mating partners because the reproductive success of Serengeti females increases with social status, and their cubs grow at a faster rate and have a higher survival than cubs of low-ranked mothers (Golla et al., 1999; Hofer and East, 1996).

Our results indicate that high-ranked males chiefly competed for high-ranked and older females, thus leaving low-ranked recent immigrants the possibility of associating and mating with reproductively less valuable females. This suggestion is supported by observations of mating between short-tenured males and young females (East ML, Hofer H, and Wilhelm K, unpublished data). Thus it is possible that there are two parts to a male queue, with recent immigrants queuing for status and attempting to encourage younger, low-ranked females to mate with them, and males with long-term tenure and high rank competing for reproductively more valuable females. As matings are not entirely monopolized by high-ranked males, the possibility that mid- and low-ranked males can obtain mating opportunities may help stabilize long queues (Kokko and Johnstone, 1999).

A unique aspect of Serengeti clans is that group members regularly leave their territory on long-distance foraging trips to areas containing large numbers of migratory herbivores (Hofer and East, 1993a,b). As high-ranked females dominate access to food resources within the clan territory, they commute less often than females with lower social status (Hofer and East, 1993c). Similarly, immigrant males with high social status are more often inside the clan territory than lower-ranked males (East and Hofer, 1991). As a result, high-ranked males and females encounter each other more often in the clan territory than lower-ranked animals of the opposite sex,

and this may in part explain why high-ranked females are shadowed more often than more subordinate females (Figure 4). High-ranked females are also more valuable mating partners than lower-ranked females (Golla et al., 1999; Hofer and East, 1996).

High-ranked males may shadow the female of their choice and exclude lower-ranked males from approaching her, but these actions may not be sufficient to ensure that she will chose him as her mate. Thus, a male's reproductive success may not be directly linked to his investment in building relationships and female defense, but rather to female mate choice (East et al., 1993). The strength of the bond developed between a female and a male is likely to be a factor influencing female mate choice, but other factors such as genetic quality may also be involved. The social status of immigrant males was an indicator of longevity, and thus it may be used by females as a reliable signal of male viability.

Even though Serengeti hyenas breed throughout the year, the pool of potential mates available in the clan territory is limited and constantly changing during periods when clan members commute (Hofer and East, 1993b,c). For this reason, patterns of mate choice by Serengeti males and females may be different from those in more strictly territorial populations.

Harassment

Recently, much attention has been focused on the impact of male harassment on female mate choice. It has been shown that when harassment is costly to females, females may chose mates that provide protection against harassment (Cassini, 1999; Clutton-Brock et al., 1993; Modig, 1996; Nefdt, 1995; Poole, 1989; Wikelski et al., 1996). Although female spotted hyenas are dominant to males, some male–female interactions might be viewed as harassment by males. Our results show that mid-ranked males often harassed females and that high-ranked males not only excluded subordinate males from females but that high-ranked males also formed coalitions with females to stop harassment by subordinate males. Thus it is possible that females that are shadowed or defended by high-ranked males rarely suffered harassment by subordinate males. Male harassment of females may be a form of male display that focuses the attention of the female on the male. Mid-ranked males are more likely to require attention from females than high-ranked males that have established, long-term relationships with females.

Choosing a queue

Immigrant males advertise their social status by producing a loud call or whoop (East and Hofer, 1991). High-ranked males produce more whooping bouts and longer bouts of whoops than subordinates, and as males increase in social status the rate at which they whoop increases. Thus whoops probably advertise a male's position in the social hierarchy, and potential immigrants may use whooping behavior to assess the lengths of queues in different clans (East and Hofer, 1991).

Immigrant males required several years of tenure before they acquired the alpha position. The number of years required to obtain the alpha position was greater in larger clans with longer queues than in smaller clans with shorter queues. If mating opportunities within a clan are chiefly monopolized by the alpha male, as suggested by Frank (1986), then it might be expected that immigrant males should seek to join the clan with the shortest male queue. If, however, the alpha male does not monopolize matings, the dispersing males should not only consider the length of queues in the clans they may join, but also the number of female clan members (i.e., potential mates). A model by Kok-

ko and Sutherland (1998) shows that it pays to join a longer queue when the amount of resource awaiting is greater than that associated with a shorter queue.

If the difference in the responses of young and old females to short- and long-tenured males reflected mating opportunities, then the number of young females that recently entered the breeding population rather than the total number of females might be the relevant measure for a dispersing male assessing which queue to join. If dispersing males focus on the number of young females per clan and distribute themselves in an ideal free manner (Sutherland, 1996), male immigration would track female recruitment and lead to a balanced adult sex ratio, as seen in Serengeti clans (Hofer and East, 1993a). Male choice of queue would then regulate the adult sex ratio in clans.

Inbreeding

If males with long tenure chiefly mate with experienced females, they are less likely to mate with their own offspring. Alternatively, if males can identify their female offspring, then older males might be expected to associate with female cubs that they have not sired, with the view to developing associations with possible future breeding partners. Because high-ranked males are more tolerated by clan females close to the communal den (East and Hofer, 1991) and high-ranked males often greet and associate with female cubs and subadults at the den (East et al., 1993), high-ranked males appear to have a better opportunity to foster associations with female cubs and subadults than lower-ranked males.

Natal nondisperser males

Prior to this study it was thought that male spotted hyenas always disperse from their natal groups (Frank, 1986; Kruuk, 1972; Mills, 1990). However, in all three study clans there were natal males that did not disperse, suggesting that this was a rare but not unusual phenomenon in the Serengeti population. In contrast to immigrant males, such nondisperser males acquired top rank in the male social hierarchy when they began to compete with immigrant males for access to females. The fact that relatively young nondispersers acquired high rank suggests that queue stability is not maintained by age asymmetries among males. Genetic analysis of paternity has demonstrated that natal nondisperser males fathered cubs (East et al., unpublished data); thus a lack of dispersal did not prevent successful reproduction. It is probable that natal nondisperser males gain immediate high rank in the male hierarchy due to the social dominance they acquire from their mother over all immigrant males during their development. Even though predispersal natal males are dominant to female clan members ranked below their mothers, these males are socially subordinate to such females when they become nondisperser males.

During this study, sons of mid- and low-ranked females became nondispersers, whereas all sons of high-ranked females dispersed. As mentioned previously, males compete for mating opportunities with high-ranked females, probably because they are the most valuable mating partners. It may be that to avoid inbreeding, high-ranked females are unlikely to mate with male relatives, but will mate with nonrelated natal males. If so, sons of high-ranked females that want to mate with high-ranked females must disperse from their natal clan.

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