COMMENTARY

Hyena politics: The dynamics of dynasties

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In most species, individual attributes such as size, strength, and condition influence individuals' ability to monopolize resources [resource-holding power (RHP)] and establish high-ranking positions in dominance hierarchies (1). But there are some taxa in which dominance rank becomes decoupled from individual differences in RHP. For example, in the eusocial wasp *Liostenogaster flavolineata*, females queue for the breeding position, with older females having priority over younger ones (2). In large provisioned groups of rhesus macaques (*Macaca mulatta*), male rank is based on the length of residence in the group (3). In some cercopithecine primates (i.e., macaques, baboons, and vervets), females inherit their mothers' ranks and form corporate matrilineal dominance hierarchies in which members of matrilines hold adjacent ranks (4). Attribute-based hierarchies tend to fluctuate as individuals' physical abilities change over time and as high-ranking individuals are challenged and replaced by more-powerful rivals (1). In contrast, the conventional matrilineal dominance hierarchies of baboons, macaques, and vervets are remarkably stable over long periods of time (4). In PNAS, Strauss and Holekamp (5) explore the dynamics and long-term consequences of matrilineal dominance hierarchies among female spotted hyenas (*Crocuta crocuta*).

Spotted hyenas live in large multimale, multifemale groups, or clans (6). Females normally remain in their clans throughout their lives, while males disperse when they reach sexual maturity. In contrast to most other social vertebrates, females outrank males. Clans are composed of multiple matrilines, which forage separately but collectively defend a shared territory. Spotted hyenas feed primarily on large and medium-sized prey that they kill themselves but may scavenge when opportunities arise (7).

There has been striking convergence in the patterns and mechanisms of maternal rank inheritance in monkeys and spotted hyenas. In both cases, two inheritance "rules" typically hold: (*i*) mothers rank above their daughters, and (*ii*) younger females outrank their older sisters (4, 8). There are also similarities in the mechanisms that underlie rank inheritance. Mothers and (and sometimes older sisters) support juveniles in conflicts with members of lower-ranking families, and this enables young females to dominate all females that their mothers and sisters outrank (4, 8). Mothers also support their younger daughters in conflicts against their older daughters, which results in sisters being ranked in inverse order of their ages.

Building Dynasties

For monkeys and spotted hyenas, there are far-reaching consequences of this process. High-ranking female monkeys generally reproduce more successfully than lower-ranking females (9). High-ranking female hyenas have higher lifetime reproductive success than lower-ranking females (5) because they begin breeding at younger ages, are more capable of sustaining concurrent pregnancies and lactation, have shorter interbirth intervals, and produce more surviving offspring than low-ranking females (10).

The combination of high-rank stability and rank-related differences in reproductive success can have profound effects on the composition of groups over time. Daughters of high-ranking females will grow up to become high ranking and reproductively successful themselves, while the daughters of low-ranking females will become low ranking and reproduce relatively unsuccessfully. If no other processes are operating, high-ranking lineages will expand and low-ranking lineages will shrink.

Strauss and Holekamp (5) document how this process played out in one of their study groups over a 27-y period. The group was originally composed of multiple matrilines, but by the end of the study period, only members of four highest-ranking lineages from the original group remained. While some of the lower-ranking lineages became extinct, others apparently left the original group. Despite these losses, the clan doubled in size over the course of the study. This growth was not distributed equally across lineages. The top-ranked lineage grew from two females in 1988 to 21 females in 2014, a 10-fold increase. The second-ranked lineage increased ninefold over this period,

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while the third- and fourth-ranked lineages each doubled in size. One of the consequences of the differential growth of lineages was that the initial rank differences among females within and across lineages were exaggerated as young females matured and were slotted into the dominance hierarchy below their mothers and above their older sisters.

Maintaining the Status Quo

These dramatic differences in the fortune of lineages raise an obvious puzzle: Females have a powerful incentive to increase their rank but do not often challenge higher-ranking females. Why don't females rebel against the status quo and challenge the established rank order?

Rebellions may be uncommon because females collectively resist challenges. In both monkeys and hyenas, females tend to support close maternal kin in conflicts. High-ranking matrilines are likely to be larger than lower-ranking lineages because of the relationship between dominance rank and reproductive success. This means that higher-ranking matrilines may be able to overpower members of lower-ranking lineages. But the correlation between lineage rank and size is often imperfect; lower-ranking matrilines sometimes outnumber higher-ranking matrilines and should be able to mount successful challenges against them. If females consistently took advantage of these discrepancies, then hierarchies would change whenever stochastic processes distorted the normal relationship between lineage rank and size.

It is also possible that rebellions are uncommon because they have little chance of success. This may be the case if group members generally have an interest in preserving the status quo and are prepared to defend it (4). If females are mainly interested in maintaining their own positions, they should be largely indifferent to the outcome of conflicts among females who rank lower than themselves. However, females typically intervene on behalf of the higher-ranking of two opponents. This suggests that social instability may be costly to all group members, even those that are not directly involved in rank challenges. For instance, during a period of social instability that led to substantial changes in the dominance hierarchy in a group of yellow baboons, there were a number of violent fights among females. Nearly all of the females in the group sustained wounds (11), even though not all of them were directly involved in the rank challenges. If rebellions create widespread collateral damage, group members may benefit from defending the established rank order.

Although these forces may reduce the likelihood that rank challenges will be successful, some females do manage to defy their matrilineal destiny. The literature contains scattered reports of revolutionary changes in matrilineal dominance hierarchies but does not provide much insight about the factors that influence successful revolts. Strauss and Holekamp (5) combine their long-term data on female dominance rank with information about coalitionary behavior to identify the elements of successful rank reversals. They find that ∼15% of the yearly rank assignments involved a reversal in relative rank, and nearly half the females in their study population were affected by rank reversals at some point in their lives. These figures do not include the rule-based rank reversals among sisters.

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Key to Successful Revolts

Coalitionary support from steadfast partners seems to be the key to successful rebellions. Females who support each other more are more likely to participate in coalitions directed at higher-ranking females, and those that receive the most support from their primary coalition partners experience the greatest positive rank changes. Strauss and Holekamp (5) interpret these results to mean that "as individuals engage in more coalitions together, they become more willing to support one another in challenging dominant individuals" (3). Patterns of coalitionary support in Old World monkeys suggest an alternate interpretation: Kinship may influence both the frequency and coalitionary support and the costs that females are willing to incur when they cooperate (4). Either way, females do not seem to be able to rise in rank without others' help.

Lessons Hyenas Teach Us

The analyses that Strauss and Holekamp (5) present offer a larger lesson about the effects of conventional systems for resolving conflicts of interest between individuals. Hierarchies that are based on inherited privilege are likely to have more lasting impacts than hierarchies based on other types of conventions, such as age and tenure. This is because the properties that confer success (and fitness advantages) are transmitted from parents to offspring. A female hyena (or baboon) who is lucky enough to be born into a high-ranking family will become high ranking and reproduce successfully herself. However, a female wasp who queues for the top-ranking position in her group will produce daughters who must still wait for their own turn at the top. Dynastic systems, like those of spotted hyenas, which combine inheritance of traits that confer fitness advantages with limited opportunities for social mobility, generate inequality that will be perpetuated and magnified across generations.

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