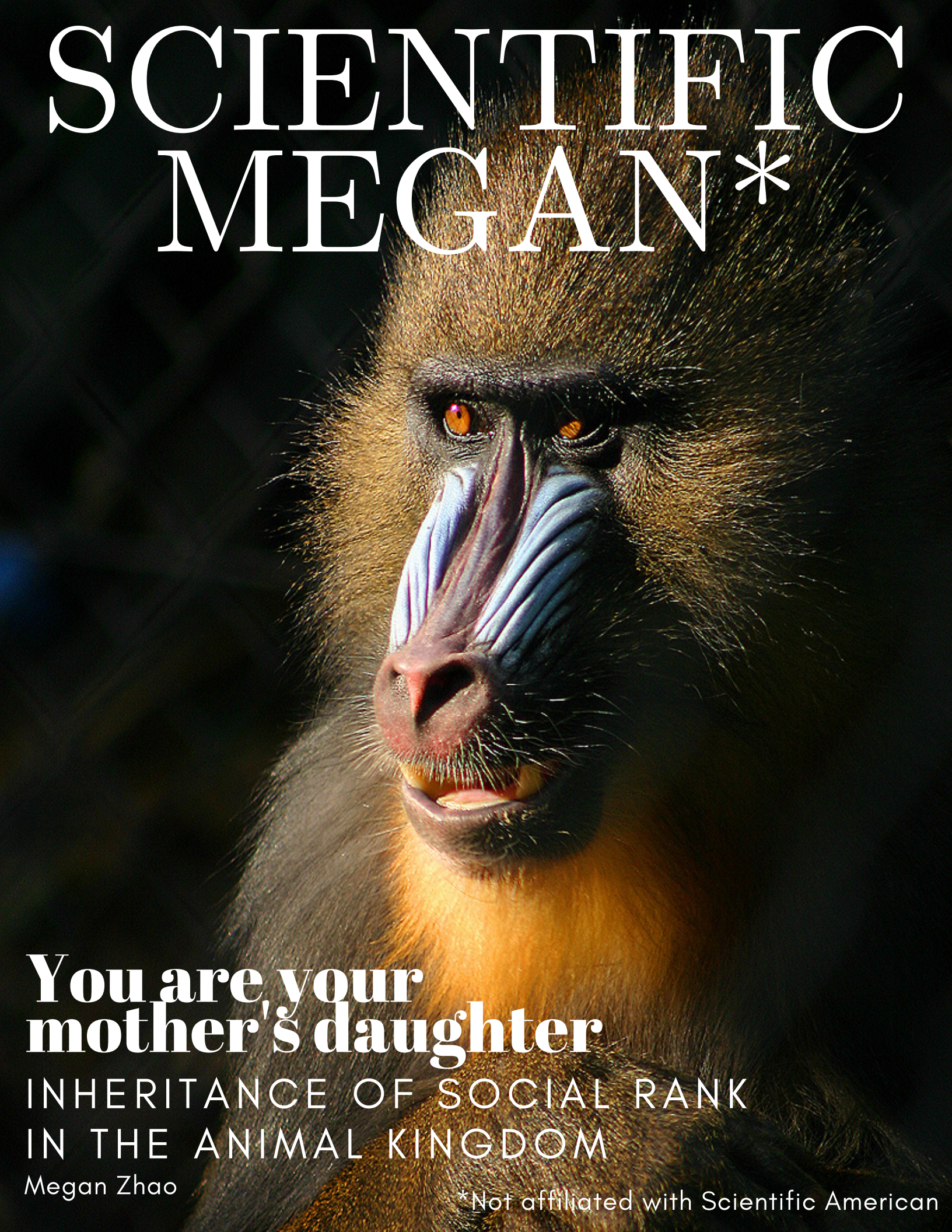
SCIENTIFIC MEGAN*



You are your mother's daughter

INHERITANCE OF SOCIAL RANK IN THE ANIMAL KINGDOM

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"Everything the light touches is our kingdom..." Mufasa says to Simba as they sit together, watching the sun rise over the plains of Africa. The story of The Lion King is known and loved by all generations, but just how realistic is Simba's story? In nature, do animals exhibit social ranks, and if so, do more highly-ranked individuals pass on their "power" to their offspring, the way Mufasa was ready to pass his kingdom on to young Simba? By studying different populations of social animals that form dominance hierarchies, animal behavior scientists have found that the inheritance of power in the animal kingdom is not as simple as Disney's portrayal. Big surprise, right?

In social animals that live the majority of their lives in the presence of others, hierarchies can be beneficial. Let's pretend you live in a group with others in the same geographic region. Everyone in your group has the same resource needs—you all need water, food, space to move around, and eventually, mates. Though some resources may be widespread and do not cause competition between you and your group mates, there may be one or two resources that are highly coveted, such as the biggest room in the apartment or the slice of pizza with the most toppings. The most important thing for your own survival, then, would be to maximize your access to and maintenance of said resource, and your ability to do this is what biologists refer to as "resource holding potential" (RHP).

Continuing this thought experiment, imagine that you are now competing against everyone in your group for a limited amount of a coveted resource. You know your own abilities, but you do not know how your RHP compares to your peers. One way to solve this problem is to "duke it out" every time this resource is available. A second option is to remember the outcome of the first several encounters, and in future encounters to only instigate fights against individuals that are more likely to lose against you. The former option creates an unstable group dynamic that can be downright chaotic, while the latter option allows the emergence of a natural hierarchy that maintains stability within the group. Social hierarchies in group-living animals is beneficial to each individual involved—the strongest get first access to resources, while the weakest have a lower probability of getting injured in high-stakes aggressive encounters.

Hierarchies have evolved across many species ranging from wasps to primates, but the path taken is not always the same. Specifically, hierarchy can be based on individual competitive ability or nepotistic inheritance. As the name suggests, individual competitive ability refers to characteristics of an individual that make them more likely to win aggressive encounters (Johnson 1987). This can be body size, stamina, agility, or any other feature that stems from the animal's physical dominance over another. On the other hand, nepotistic inheritance is much more reminiscent of human relationships—an individual's rank in the group is based on their family, and how their family is ranked in the group.

The Dominance Gene?

If you're scratching your head wondering why this illogical "youngest ascendancy" pattern exists, you're not alone. It may help to discuss the mechanism behind rank inheritance, and the environmental conditions that may make nepotistic inheritance more likely to occur. When the word "inheritance" comes up in biology, the knee-jerk response is to think of genetic inheritance, and for good reason. One of the tenets of evolution by natural selection is that a trait must be heritable to make a difference in the bigger picture, and more often than not, this depends on genetic inheritance of traits that confer a fitness benefit. Social rank inheritance is one case that cannot be fully explained by genetic inheritance. In multiple species of primates, if a mother's rank changes, her offspring's ranks change as well, and continue to follow the pattern previously described (Holekamp and Smale 1991). This suggests that genetic information has little to no influence on social rank inheritance in matrilineal primate species.

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In other words, nepotistic inheritance is all about who you know, not what you can do (Lea et al. 2014).

In the case of Simba's inheritance of Mufasa's kingdom, nepotistic inheritance clearly dominates. Nepotistic inheritance is not limited to Disney movies, the monarchy, or your next networking event; it is a somewhat counterintuitive approach to maintaining stability within social animals. Nepotistic inheritance occurs in multiple species of Cerpothecinae, or Old World monkeys, as well as spotted hyaenas. The species in which nepotistic inheritance has been observed all point towards a similar pattern: female offspring inherit a rank immediately below their mother's, with siblings often exhibiting "youngest ascendancy," meaning the youngest offspring is ranked highest, with each older sibling ranked below her in order of increasing age (Lea et al. 2014).

The correlation between gene expression and dominance rank is less clear cut for males of matrilineal primate species, as demonstrated by Lea and colleagues in baboons. Like many other Cerpothecenine species, female baboons exhibit nepotistic inheritance, but male baboon hierarchies are based on fighting ability (Lea et al. 2018).

Therefore, one may expect that dominant males are larger and stronger than their lower-ranked peers, however, the story got much more interesting when the researchers looked beyond the immediate phenotypic differences between male baboons of different ranks. Specifically, highly-ranked male baboons have higher expression of genes associated with innate immunity, and the research team demonstrated that this pattern of gene expression is a precursor to high social status, and not a consequence of it (Lea et al. 2018). Though this particular case may suggest high social status is "inherited" in the form of differential gene expression, it is more accurate to say this form of hierarchy is based on individual competitive ability, and not nepotistic inheritance.

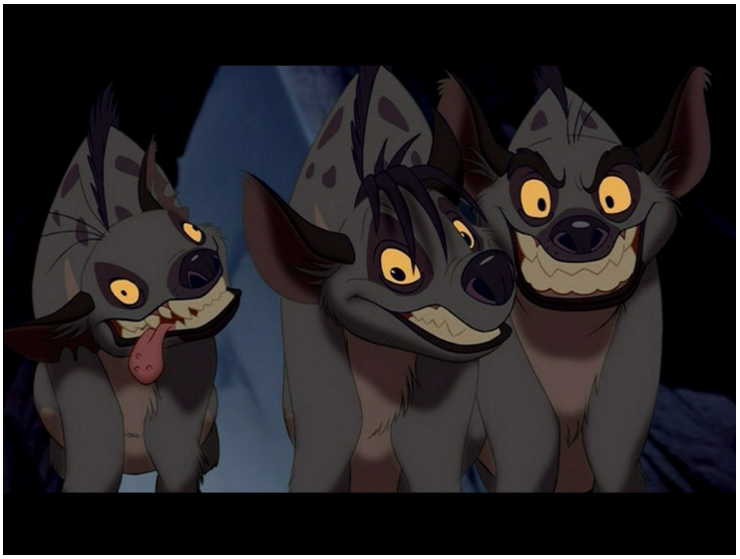
How and why does nepotistic inheritance happen?

Although there are no clear answers as to why nepotistic inheritance of social rank evolved as opposed to hierarchies based on individual competitive ability, animal behavior researchers are learning more and more about the likeliest explanation for how ranks are inherited. Here's the bad news—it may be time to finally accept your mother's help, because the degree of maternal intervention in agonistic encounters is the strongest predictor for social rank inheritance (Holekamp and Smale 1991). In vervets, highly ranked mothers interfered more frequently in disputes involving their offspring, and significantly, mothers never intervened in encounters involving individuals of higher rank (Holekamp and Smale 1991). Similarly, in spotted hyaenas, higher-ranked mothers intervened more effectively than their lower-ranked counterparts (Engh et al. 2000). In fact, higher-ranked cubs were harassed less frequently than low-ranked cubs, indicating that though low-ranked mothers had more opportunity to intervene, they chose not to (Engh et al. 2000). The mechanism of maternal intervention makes sense in the context of the "youngest ascendancy" pattern of inheritance because mothers are more likely to pay attention to new offspring that are more vulnerable to agonistic encounters.

Steve Bloom: Photographing our living world

Given the evidence of maternal interference in offspring's disputes as a predictor of social rank, we have set the stage to ask the question of why nepotistic inheritance has evolved in multiple species. Equal access is all the rage in modern human society, so it may seem counterproductive to us to construct hierarchies, especially nepotistic ones that do not reward hard work and only reward blood line. However, there are compelling reasons for why the same patterns of nepotistic inheritance persist in multiple species. Equal access to resources is not problem when food is abundant and widely dispersed, and relationships with other group members offer few benefits in gaining access to readily available resources. On the other hand, for animals that have limited access to resources, stable linear dominance hierarchies improve the overall fitness of the group. Though likely not the case for Cercopithecine primates, nepotistic hierarchies may be likelier to evolve when resources are clumped and can be

monopolized by single individuals. As a result, nepotistic hierarchies can evolve when related individuals gain benefits from helping their relatives, whether directly or indirectly (Johnson 1987). For example, a mother may experience benefits later in life for interfering more often in her offspring's agonistic encounters with other members of the group. Therefore, individuals undergo selection to help their kin attain resources or win fights (Archie et al. 2006).



The Lion King

What does this mean for Simba?

There are many unanswered questions in the study of dominance relationships in animals. For example, why do lower-ranking females put up with this system? Or, how exactly does the availability of resources translate to rank inheritance? Unfortunately for Simba, what we do know is that no cases of nepotistic inheritance have been observed in lions, and in general, it is rare for nepotistic inheritance to occur in males of any species. Perhaps the next remake of The Lion King should reframe the story through Nala's lens, or take it one step farther in accuracy and follow Scar's band of cackling hyaenas instead.

References

Archie, Elizabeth A., Thomas A. Morrison, Charles A.H. Foley, Cynthia J. Moss, and Susan C. Alberts. 2006. "Dominance Rank Relationships among Wild Female African Elephants, Loxodonta Africana." Animal Behaviour 71 (1): 117–27. https://doi.org/10.1016/j.anbehav.2005.03.023.

Engh, Anne L., Katrina Esch, Laura Smale, and Kay E. Holekamp. 2000. "Mechanisms of Maternal Rank 'Inheritance' in the Spotted Hyaena, Crocuta Crocuta." Animal Behaviour 60 (3): 323–32. https://doi.org/10.1006/anbe.2000.1502.

Holekamp, Kay E., and Laura Smale. 1991. "Dominance Acquisition During Mammalian Social Development: The 'Inheritance' of Maternal Rank." American Zoologist 31 (2): 306–17. https://doi.org/10.1093/icb/31.2.306.

Johnson, Julie A. 1987. "Dominance Rank in Juvenile Olive Baboons, Papio Anubis: The Influence of Gender, Size, Maternal Rank and Orphaning." Animal Behaviour 35 (6): 1694–1708. https://doi.org/10.1016/S0003-3472(87)80062-3

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Lea, Amanda J., Mercy Y. Akinyi, Ruth Nyakundi, Peter Mareri, Fred Nyundo, Thomas Kariuki, Susan C. Alberts, Elizabeth A. Archie, and Jenny Tung. 2018. "Dominance Rank-Associated Gene Expression Is Widespread, Sex-Specific, and a Precursor to High Social Status in Wild Male Baboons." Proceedings of the National Academy of Sciences 115 (52): E12163–71. https://doi.org/10.1073/pnas.1811967115.

Lea, Amanda J., Niki H. Learn, Marcus J. Theus, Jeanne Altmann, and Susan C. Alberts. 2014. "Complex Sources of Variance in Female Dominance Rank in a Nepotistic Society." Animal Behaviour 94 (August): 87–99. https://doi.org/10.1016/j.anbehav.2014.05.019.