Acknowledgments: We thank B. Bingham and J. See for assistance with the initial anatomical experiments; R. Fallon, G. Sartor, L. Zhang, S. Mahler, K. Moussawi, R. Smith, and T. Smith for assistance with behavioral studies; C. Bäckman and W. Freed for use of their microscopy equipment; and C. Mejias-Aponte for his programming expertise and thoughtful comments. This work was supported by U.S. Public Health Service grant awards R37-DA006214 and F31-MH071093, and the National Institute on Drug Abuse Intramural Research Program. The anatomical data were gathered at the University of Pennsylvania.

Supporting Online Material
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21 February 2011; accepted 1 June 2011
10.1126/science.1204622

Life at the Top: Rank and Stress in Wild Male Baboons

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In social hierarchies, dominant individuals experience reproductive and health benefits, but the costs of social dominance remain a topic of debate. Prevailing hypotheses predict that higher-ranking males experience higher testosterone and glucocorticoid (stress hormone) levels than lower-ranking males when hierarchies are unstable but not otherwise. In this long-term study of rank-related stress in a natural population of savannah baboons (*Papio cynocephalus*), high-ranking males had higher testosterone and lower glucocorticoid levels than other males, regardless of hierarchy stability. The singular exception was for the highest-ranking (alpha) males, who exhibited both high testosterone and high glucocorticoid levels. In particular, alpha males exhibited much higher stress hormone levels than second-ranking (beta) males, suggesting that being at the very top may be more costly than previously thought.

In many animal societies, a high dominance rank is beneficial (*1*, *2*). High-ranking primates, for example, tend to experience higher reproductive success and/or greater offspring quality as measured by survival, growth rates, and accelerated maturation (*3*–*8*). Social rank also influences health (*9*). However, attaining and maintaining high dominance rank may entail substantial energetic costs, especially for males, if high-ranking individuals are involved in more agonistic and sexual activities (*10*).

Currently, no consensus exists about the rank-associated stress physiology of individuals in stratified mammal societies, with various studies producing apparently contradictory findings. In some studies, it is subordinate animals, and in others it is dominants, that exhibit greater stress levels (*11*, *12*). These differences may arise from species-level variations in social and mating systems or from variability in study methodology and animal housing (*11*, *12*). Differences within social and mating systems, or even within species, may also occur as a function of hierarchy stability (*13*). For example, in a pioneering investigation, Sapolsky (*13*, *14*), studying wild olive baboons, determined a male dominance hierarchy during each of seven annual 3-month research periods. During research periods when the hierarchy was stable, high social ranks were associated with lower levels of glucocorticoids, but this advantage was lost during a research period when the hierarchy was unstable (when a high proportion of agonistic interactions involved "reversals": a subordinate winning over a dominant male) (*13*, *14*). Two other investigations of multi-male primate societies defined unstable periods as those in which rank changes occurred for males that were in the alpha position (semi-captive mandrills) (*15*) or in either the alpha and/or beta position (wild chacma baboons) (*16*). Both studies found an interaction between dominance and stability, although the relationship between rank and fecal glucocorticoids (fGCs) within periods was significant in only one of the two studies, perhaps because of differences in sample size. In contrast to those three studies, high-ranking chimpanzee males had higher glucocorticoid levels than did low-ranking ones during a period of stability (identified by no rank changes among adult males) (*10*).

Exposure to stressors activates a chain of endocrine reactions, including the secretion of glucocorticoids by the adrenals, which mobilizes the energy necessary to adapt to the stressor (*17*). Short-term secretion is beneficial, but long-term exposure to high levels can lead to suppressed immune function (*15*, *18*). Glucocorticoids can also suppress testosterone (*9*, *17*), which is the major steroid contributing to sperm production, muscle mass, male secondary sexual characteristics, and sexual and aggressive behaviors (*19*–*21*). However, under some conditions, including mating in seasonally breeding species or in high-ranking

Table 1. Effect of hierarchy stability and social dominance on hormone concentrations. Statistically significant (sig.) results appear in bold. *b*, is the parameter estimate.

Variables*	*b*	Numerator df	Denominator df	*F*	Sig.
		Dependent variable: log fGCs			
Intercept		1	429.665	4758.378	<0.001
Dominance rank	**0.0043**	**1**	**1578.129**	**5.390**	**0.020**
Alpha status	**0.0437†**	**1**	**2334.854**	**9.134**	**0.003**
Hierarchy stability	**–0.0182‡**	**1**	**2351.302**	**5.666**	**0.017**
Season	**–0.0239§**	**1**	**2324.398**	**9.100**	**0.003**
Temperature	–0.0062‖	1	2337.664	0.393	0.531
Age	0.0034	1	522.355	2.153	0.143
		Dependent variable: log ft			
Intercept		1	625.525	3891.482	<0.001
Dominance rank	**–0.0124**	**1**	**2374.909**	**29.102**	**<0.001**
Alpha status	–0.0117†	1	2360.698	0.473	0.492
Hierarchy stability	0.0146‡	1	2301.445	2.776	0.096
Season	**0.0705§**	**1**	**2290.120**	**60.702**	**<0.001**
Temperature	**0.0266¶**	**1**	**2294.284**	**5.481**	**0.019**
Age	**–0.0249**	**1**	**1816.997**	**59.963**	**<0.001**

*Factors that were not significant for either hormone were dropped. These included the interaction between rank and hierarchy stability (a fixed factor) and social group (a random factor). For the four categorical variables (alpha status, hierarchy stability, season, and temperature), a positive value of *b* indicates that the hormone concentration was higher †for the alpha male, ‡when the hierarchy was stable, §during the wet season, ¶in cooler months. The variable "dominance rank" captures the linear component of the functional relationship between rank and the hormones; the binary variable "alpha status" captures the nonlinear component.

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