Supporting Online Material for

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

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This PDF file includes:

Online supplement of Methods section

Study population and field site

Baboons are large cercopithecine primates that form relatively permanent multimale-multifemale groups consisting of 10 to 200 individuals. Breeding and births regularly occur in all months of the year. Both males and females exhibit linear dominance hierarchies, and adult males are dominant to all other age-sex classes. Infants are born after six months gestation, and inter-birth intervals are approximately two years. Adolescence lasts from about six to eight years of age for males, after which time males reach full adulthood, experience dispersal from their natal group, and rapidly rise in dominance rank (S1). Adult males weigh approximately 25 kg, about double the weight of adult females. By approximately 10-12 years of age, males begin to decline in rank, in testosterone levels, and in offspring production. Secondary dispersal by males is common throughout adulthood (S2-S6).

The Amboseli basin, Kenya, is a semi-arid open grassland savannah with scattered trees 2º40' south of the equator. The region experiences a predictable five-month dry season (June-October) that is essentially devoid of rain, and a wet season (November-May) in which an average of 350mm of rain falls per year (S7-S9). Some months are also characterized by high ambient temperature, with maximum daily air temperatures in the shade sometimes exceeding baboons' normal core body temperature of 38°C (S9). Individuals in the Amboseli baboon study population are monitored on a near-daily basis. Life-history and behavioral data have been collected since 1971, weather data since 1976, and noninvasive fecal sampling since late 1999 (S10).

Hormone data

Fecal sample collection, storage, and extraction were performed as described previously (S11, S12). The samples were then assayed for glucocorticoid (fGC) and testosterone metabolites (fT) using radioimmunoassays (S6, S8-S10). For this study we used all fGC and fT data for adult males from January 2000 through December 2008.

Dominance ranks and rank stability

Male dominance rank was determined monthly for each male by creating matrices of wins and losses using outcomes of dyadic agonistic encounters between males (S13). We then ordered the rows and columns to minimize occurrences below the main diagonal. Constructing the hierarchy this way on a monthly basis results in a ranking that is linear and transitive and a dominance matrix with very few 'reversals', i.e entries below the main diagonal (S3). Each male was then assigned an ordinal dominance rank starting with the highest ranking or alpha male as 1, the beta male as 2, and the lowest ranking male as the number of males higher than him +1.

For each group, the male dominance hierarchy for each month was then categorized as stable or unstable. Definitions of dominance stability have not always been explicit in the literature and where they have been, no consistent definition has been used. Here, we considered a measure of stability similar to the one used by Setchell (S14) and Bergman (S15) who used change in rank as their measure of stability, but we extended this change in rank to the top three positions instead of only the rank 1 (S14) or rank 1 and 2 males (S15). We chose three males in particular because the top three ranking males in a social group account for nearly 70% of conceptions in a group on average (S16), indicating that they are monopolizing the majority of the reproductive

opportunities in the group. A month was considered to be stable if males in each of the top three positions were the same as month before and the month after.

One study group, Omo, had fewer than three adult males for part of the study (Jan 2000 through Jan 2004, and in Mar and Apr 2004); we excluded samples for those months for that group. Using the stability criterion previously described, approximately 46% of our study months were stable (223 stable, 262 unstable); mean duration of stable periods was three months (range 1- 15). We note that findings reported here were similar if we use even more stringent stability criteria, such as five or six months without change in the top three rank positions rather than three months (results not shown).

Agonism (aggressive-submissive), challenges (reversals), grooming received, and consortships (mate-guarding episodes)

As part of our regular monitoring of each study group, dyadic agonistic encounters between adult males were recorded *ad libitum* throughout the six-hour observation sessions on each group several days per week, primarily by three long-term observers (total of 58 observer-years experience) (S10). Because sampling was *ad libitum*, the overall number of agonistic encounters observed in any month and group may vary. However, because of the observer movement patterns and experience, and because of Amboseli's open savannah habitat, we are confident that we were not less likely to observe interactions involving the beta male, when they occurred, than we were to observe interactions involving the alpha male. Consequently, comparisons of agonistic behavior for alpha and beta males were based on pairing individuals by group and month. For each alpha and beta male, we calculated the sum of all records of his agonistic encounters with other adult males (including both wins and losses) for each month.

Data for multiple months for the same alpha-beta pair were then averaged so that each pair contributed only a single value in the analysis. Pairs that persisted for at least three months of observation were included unless no male-male agonisms were observed for either member of the pair during that time. The result was data for 54 alpha-beta pairs.

The proportion of challenges to alpha and beta males was also determined using the agonism data. Using the dominance ranking determined for each month, we then calculated the number of agonistic encounters each alpha or beta male won or lost each month against the three nearest lower-ranking males (S17). For each alpha-beta pair, the proportion of challenges was then calculated as the proportion of total agonistic interactions that alpha and beta males lost against the three nearest lower-ranking males (S17). Pairs that persisted for at least three months of observation were included unless neither member of the male pair had a reversal during that time. The result was data for 29 alpha-beta pairs.

Because we calculate dominance rankings on a monthly basis rather than over several months as in some other studies (S17, S18), many reversals or 'challenges' that occur (wins by a lower ranking male against a higher ranking opponent) appear in our data as rank changes that occur from month to month. That is, when one member of a pair of adjacently ranked males wins the majority of that pair's agonistic interactions in a given month, we typically designate him as having attained rank over the other member of the pair that month. Consequently, less than 4% of the total interactions among adult males in our analysis appear as instances in which the lower ranking member of a pair won an interaction with the higher ranking member but remained the lower ranking of the two. We incorporated our definition of "stability" (rank changes among the top three males) in our GLMM, and we incorporated reversals or 'challenges' (instances in which the lower ranking member of a pair won an interaction with the

higher ranking member but remained the lower ranking) in our comparison of alpha and beta males. By doing so, we capture the major, distinct features of "stability" as defined by several other authors (S14, S15, S17).

Grooming episodes given to adult males by adult females were recorded *ad libitum* (S10); we are confident that we were as likely to observe the alpha male when he was being groomed as we were to observe the beta male when he was being groomed, i.e., that observers were not biased towards observing either the alpha or beta male. Consequently, comparisons of grooming received by alpha and beta males, like comparisons of agonistic interactions, were based on pairing individuals by group and month. For each alpha and beta male, we calculated the sum of all records of grooming by adult females for each month and then calculated an average within each alpha-beta pair as for the other behavior analyses. Pairs that persisted for at least three months of observation were included unless neither member of the male pair was observed being groomed during that time. The result was data for 53 alpha-beta pairs.

Sexual consortships are easily observable mate-guarding episodes during which an adult male maintains close spatial proximity to, follows, grooms, and mates with an estrous female while also keeping other males away from the female (S3, S13, S19). Consortships are energetically costly for the male because they reduce foraging and resting time (S20, S21). As part of our regular monitoring of each study group, all occurrences of sexual consortships were recorded (S10, S20-S22). Each record includes the onset and termination of the consortship (or, for censored bouts the start time and end time of the day's observations). For each alpha and beta male in each month we calculated the total monthly time spent in consortship by adding the duration of all consortships for that male. Observation time is equal for all males in the same group in a given month; as with the agonism data, consort time was examined in a paired

analysis comparing alpha and beta males in the same group during the same month. Data for multiple months for any alpha-beta pair were averaged so that each pair contributed only a single value in the analysis. Pairs that persisted for at least three months of observation were included unless no consortships were observed for either member of the pair during that time. The result was data for 53 alpha-beta pairs.

Data Analyses

Hormone values were log transformed to approach normality. Because fecal samples were collected *ad libitum* (no more than 1/day/male, total 4543 samples for 125 males), sample numbers were variable across males and months. To reduce the effect of uneven sampling, we first calculated for each male an average fGC and fT level within each month, resulting in 2432 monthly values (mean 19 monthly values per male, range 1-69); we then used month as the temporal unit in our analyses. Second, we built General Linear Mixed Models (GLMM), one for fGC and another for fT using SPSS 17.0. Dominance rank and rank stability, the variables of focus, were entered as fixed factors as was an interaction between rank and rank stability. Based on the form of the distribution, non-linearity was evaluated by using a binary rank variable alpha/other ranks. In addition, environmental factors (wet/dry season and cool/hot month) and age were included as fixed factors in each model based on literature for diverse species and on our recent results for this population (S9). In each GLMM model, baboon identity and group membership were included as random factors. Factors that were not significant for either hormone were dropped from the final models. For fixed factors, this was the case for the interaction between rank and rank stability; for random factors, this was the case for group. Because results were not affected by inclusion of factors that were significant for just one hormone (e.g., temperature), we retained these for both hormones to facilitate comparison.

Graphic depiction of a particular variable's effect, such as the effect of dominance rank, is provided in the figures following the common (but inexact) technique of using the residual values given by a reduced GLMM in which that parameter was not included. Note that such visualizations are not a substitute for the full statistical model results. The exact values for the effects are found in the full statistical model reported in Table 1. Plots such as Figs 1&2 that are focused on visualizing the effects of a single variable (rank in our case) are included because almost all readers other than statisticians find them a more intuitive and satisfying way of getting a feel for the statistical results of the model. Graphing residuals from a reduced model is the overwhelmingly common, albeit imperfect, method for creating such visuals, and we have done so here because the underlying structure of the variables in our case results in graphs that retain the major features of the statistical relationships even though the exact model values will not be identical to the residual ones.

The paired comparison of alpha *vs.* beta males for the four behavioral measures (proportion of challenges, frequency of being groomed, agonism rate and consort time) were performed using the non-parametric Wilcoxon Signed rank-test.

References

S1. M. J. E. Charpentier, J. Tung, J. Altmann, S. C. Alberts, Age at maturity in wild baboons: genetic, environmental and demographic influences. *Mol. Ecol.* **17**, 2026–2040 (2008).

S2. A. E. Pusey, C. Packer, in *Primate Societies*, B. B. Smuts, D. L. Cheney, R. M. Seyfarth, R. W. Wrangham, T. T. Struhsaker, Eds. (Univ. Chicago Press, Chicago, IL, 1987), pp. 250-266.

S3. S. C. Alberts, H. E. Watts, J. Altmann, Queuing and queue-jumping: long-term patterns of reproductive skew among male savannah baboons. *Anim. Behav.* **65**, 821-840 (2003).

S4. L. Swedell, S. R. Leigh, Eds., *Reproduction and Fitness in Baboons: Behavioral, Ecological, and Life History Perspectives* (Univ. Chicago Press, Chicago, IL, 2006).

S5. C. J. Jolly, *in Primates in Perspective,* C. J. Campbell, A. Fuentes, K. C. MacKinnon, M. Panger, S. K. Bearder, Eds., (Oxford Univ. Press, New York, 2007), pp. 240-251.

S6. J. Beehner, *et al*., Testosterone related to age and life-history stages in male baboons and geladas. *Horm. Behav.* **56**, 472-480 (2009).

S7. S. C. Alberts, *et al.,* in *Primate Seasonality: Implications for Human Evolution,* Brockman D.K. & van Schaik C.P., Eds., (Cambridge Univ. Press, 2005), pp. 157-196.

S8. L. R. Gesquiere, *et al.,* Coping with a challenging environment: effects of seasonal variability and reproductive status on glucocorticoid concentrations of female baboons *(Papio cynocephalus)*. *Horm. Behav.* **54**, 410-416 (2008).

S9. L. R. Gesquiere, P. Onyango, S. C. Alberts, J. Altmann J. Endocrinology of year-round reproduction in a highly seasonal habitat: environmental variability in testosterone and glucocorticoids in baboon males. *Amer. J. Phys. Anthropol*. (2010), (DOI 10.1002/ajpa.21374).

S10. See www.princeton.edu/~baboon for details in the Amboseli Monitoring Guide, and for a full publication list.

S11. M. Z. Khan, J. Altmann, S. S. Isani, J. Yu, A matter of time: evaluating the storage of fecal samples for steroid analysis. *Gen. Comp. Endocrinol*. **128**, 57-64 (2002).

S12. J. W. Lynch, M. Z. Khan, J. Altmann, M. N. Njahira, N. Rubenstein, Concentrations of four fecal steroids in wild baboons: medium-term storage conditions and consequences for data interpretation. *Gen. Comp. Endocrinol* **132**, 264-271 (2003).

S13. G. Hausfater, Dominance and Reproduction in Baboons (*Papio cynocephalus*), *Contrib. Primatol.* (Karger, Basel, 1975), Vol. 7, pp. 1-150.

S14. J. M. Setchell, T. Smith, E. J. Wickings, L. A. Knapp, Stress, social behaviour, and secondary sexual traits in a male primate. *Horm. Behav.* **58**, 720-728 (2010).

S15. T. J. Bergman, J. C. Beehner, D. L. Cheney, R. M. Seyfarth, P. L. Whitten, Correlates of stress in free-ranging male chacma baboons, *Papio hamadryas ursinus*. *Anim. Behav.* **70**, 703-713 (2005).

S16. S. C. Alberts, J. C. Buchan, J. Altmann, Sexual selection in wild baboons: from mating opportunities to paternity success. *Anim. Behav.* **72**, 1177-1196 (2006).

S17. R. M. Sapolsky, Cortisol concentrations and the social significance of rank instability among wild baboons. *Psychoneuroendocrinology* **17**, 701-702 (1992).

S18. R. M. Sapolsky, Endocrine aspects of social instability in the olive baboon *(Papio anubis*). *Am. J. Primatol.* **5**, 365-379 (1983).

S19. F. B. Bercovitch, Reproductive success in male savanna baboons. *Behav. Ecol. Sociol.* **21**, 163-172 (1987).

S20. K. L. R. Rasmussen, Changes in the activity budgets of yellow baboons (*Papio cynocephalus*) during sexual consortships. *Behav. Ecol. Sociol.* **17**, 161-170 (1985).

S21. S. C. Alberts, J. Altmann, M. L. Wilson, Mate guarding constrains foraging activity of male baboons. *Anim. Behav.* **51**, 1269-1277 (1996).

S22. J. Altmann, Observational study of behavior: sampling methods. *Behaviour* **49**, 227-267 (1974).