

The Finding of an Inverse Relationship between Social Dominance and Feeding Priority among Pairs of Unfamiliar Adult Male Vervet Monkeys (*Cercopithecus aethiops sabaesus*)

MELISSA S. GERALD
National Institutes of Health

ABSTRACT. Dominance is often presumed to confer priority of access to resources. This study evaluated the relationship between two assessments of dominance: (1) social dominance, based on agonistic interactions and (2) feeding priority among pairs of unfamiliar adult vervet monkeys (*Cercopithecus aethiops sabaesus*) differing in scrotal colour, but matched for height, weight and testicular volume, during paired introduction experiments. Results of this investigation showed that neither size differences nor scrotal colour were predictive of feeding priority, and social dominance was inversely related to feeding priority. This finding demonstrates that different assessments of dominance can yield different outcomes even within the same primate taxon. I propose that male dominance rank may best predict access to resources when there is direct contest competition over a resource, which is not immediately exhaustible, whereas highly impulsive low ranking males may gain a competitive edge in scramble competitions for ephemeral and small resources.

Key Words: Social dominance; Feeding priority; Scrotal colour; Vervet monkeys.

INTRODUCTION

The subject of how to define and measure dominance has received tremendous attention and controversy in the primate behaviour literature (ROWELL, 1974; NOË et al., 1980; BERNSTEIN, 1981; FEDIGAN, 1982). In general, status implies an asymmetrical relationship between individuals and dominance relationships are typically inferred from the outcome of agonistic interactions. Researchers often use different contexts and behavioural measures to identify dominance relationships. It is not always clear whether these differences yield comparable dominance outcomes in all primates (ROEDER & FORNASIERI, 1995) or even for the same primate taxon (NOË et al., 1980). The present study investigated the relationship between dominance as assessed by (1) agonism during introductions and (2) priority of access to resources among pairs of unfamiliar adult male vervet monkeys (*Cercopithecus aethiops sabaesus*).

As previous studies suggested that body size might be related to social status and dominance in primates (ROWELL, 1988; MENDOZA, 1993; BERCOVITCH, 1996) and recent experimental evidence revealed a relationship between scrotal colour and social dominance in vervet monkeys (GERALD, 2001), I also examined size differences and the effect of scrotal colour on feeding priority.

MATERIAL AND METHODS

STUDY POPULATION AND SUBJECTS

The subjects were 106 adult male vervet monkeys from the captive population at the

Barbados Primate Research Center and Wildlife Reserve (BPRC and WR) in St. Peter Barbados. Subjects from the BPRC and WR were passively trapped from the free-ranging population on the island of Barbados. They resided at the BPRC and WR for at least one month prior to participating in experiments.

Experiments involved introducing 53 pairs of putative strangers (subjects in a pair were from remote parishes) to eliminate effects of prior social interactions and relationships. Pairs were closely matched for height, weight and testicular volume, but differing in scrotal colour, as this study was part of a larger investigation aimed at examining the signal function of scrotal colour. Experiments herein described included the following three combinations: two Pale males ($N=19$ pairs), one Pale male and one Dark male ($N=22$ pairs), and two Dark males ($N=12$ pairs) for a total of 60 Pale males and 46 Dark males. Subjects were tested once.

EXPERIMENTS

Introduction experiments were scheduled for 90 min and terminated prematurely if animals presented a threat to each other. Previous introduction experiments in primates suggest that the dominance relationships established in this length of time can persist over a long period of time (MENDOZA, 1993). Details of experimental procedures and methods of body measurements are described extensively elsewhere (GERALD, 2001). To increase subject motivation during the feeding priority experiments, subjects were offered a small fresh apple or orange 30 min to 1 hr prior to the introduction experiments. This amounted to only a fraction of their daily breakfast, as animals are usually fed a cup of grains.

Among pairs, a Test male and a Stimulus male were designated prior to the introduction. Agonistic interactions that the Test male directed, received and mutually engaged in with the Stimulus male were recorded using continuous recording methods (ALTMANN, 1974). Social dominance within pairs was identified for each of the 53 pairs, as identified by the direction and frequency of the following agonistic behaviours: submission, avoidance (RALEIGH & MCGUIRE, 1989) and supplantation (ROWELL, 1971). For each pair, I added the number of times each male submitted, avoided and supplanted the other male. As agonistic interactions were never unidirectional, the "dominant" male was defined as the male who submitted and avoided the other male less often and/or supplanted the other male more often.

Immediately following the introduction experiments, when pair members were equidistant from the cage center, I placed one quarter of a large fresh orange or one half of a small fresh orange between the animals. A winner (i.e. the animal with feeding priority) was declared when a monkey took and ate the fruit. Once the fruit was consumed, I repeated this procedure once more. If after 10 min, neither animal ate the fruit, no winner was identified.

SCROTAL COLOUR

The scrotal colour of subjects was defined by comparing the colour found on the midpoint of the lower midsection of the scrotum with colours found on the Pantone® Process Imaging Guide 1000 (Caristadt, NJ, 2nd printing, 1992). As components of scrotal colour vary continuously in vervet monkeys and rarely is colour homogeneous (GERALD et al., 2001), colour was assigned when the author and research assistant reached agreement. To simplify, colour characterization, I used the dichotomous colour categories of 'Pale' and 'Dark,' defined by the relative darkness, also known as the colour value. The constructs, Pale and Dark, were based on the BPRC and WR population measures of lightness, as yielded from Adobe PhotoShop 4.10, a colour system built on the Pantone® Matching System. Lightness (L) ranges from 0 (black) to 100 (white). Dark males were those below the mean ($L < 91$) and males above the mean were

defined as "Pale" ($L > 92$). Those pairs who were composed of males of the same colour (Pale-Pale and Dark-Dark) were on average within 1.5 lightness values of each other, whereas pairs of males differing in colour (Pale-Dark) differed on average by 7.8 lightness values.

DATA ANALYSES

Binomial proportion tests, with the significance level set at $p < 0.05$, assessed relationships between size, scrotal colour, social dominance and feeding priority. Analyses were performed via SPSS 8.0 (Chicago, IL, 1998).

RESULTS

Among subjects in this study, Pale ($N=60$) and Dark ($N=46$) males did not statistically differ in weight (Mann Whitney, $U=1133.5$, $p=0.219$) or height ($U=120.5$, $p=0.097$) and Dark males displayed larger testicular volumes ($U=938.0$, $p=0.005$) than Pale males (Table 1). As reported elsewhere (GERALD, 2001), Dark males socially dominated Pale males ($N=22$ pairs, $p=0.017$).

A winner was declared for 53 of 53 trials in the first feeding priority trial, and for 51 of the 53 trials in the second feeding priority trial. Males who obtained the fruit slice in the first feeding priority trial were also significantly more likely to secure the fruit slice in the second trial ($N=51$, $r=0.504$, $p=0.001$).

Despite efforts to eliminate size asymmetry, individuals within a pair differed in size (mean difference: weight=0.57 kg, height=2.05 cm, and testicular volume=75.55 cc). As shown in Table 2, similar to results previously reported for social dominance (GERALD, 2001), neither weight, height, nor testicular volume were predictive of feeding priority in either Trial 1 (weight: $N=53$, $p=1.00$; height: $N=53$, $p=0.583$; testicular volume: $N=53$, $p=1.00$) or Trial 2 (weight: $N=51$, $p=0.575$; height: $N=51$, $p=0.263$; testicular volume: $N=51$, $p=0.401$). Though Dark males were socially dominant to Pale males, Dark males did not have feeding priority of

Table 1. Colour and body size measures.

Body measures	Pale	Dark
<i>N</i>	60	46
Mean weight (kg)	5.53	5.77
SE	0.0691	0.1136
Mean height (cm)	40.45	41.13
SE	0.2468	0.3018
Mean testicular volume (cc)	262.88	312.82
SE	10.53	16.62

Table 2. The relationships between weight, height, testicular volume, scrotal colour, social status, and feeding priority in Trial 1 and Trial 2.

	Trial 1		Trial 2	
	% achieves Feeding priority	Binomial test	% achieves Feeding priority	Binomial test
Weight	Lighter 27/53 (51%)	$p=1.000$	Heavier 28/51 (55%)	$p=0.575$
Height	Shorter 29/53 (55%)	$p=0.583$	Taller 30/51 (59%)	$p=0.263$
Testicular volume	Smaller 27/53 (51%)	$p=1.000$	Larger 29/51 (57%)	$p=0.401$
Scrotal colour	Pale 15/22 (68%)	$p=0.134$	Pale 14/20 (70%)	$p=0.115$
Social status	Subordinate 40/53 (75%)	$p=0.001$	Subordinate 42/52 (81%)	$p=0.001$

access to the fruit slices in either Trial 1 ($N=15$ of 22 trials, $p=0.134$) or Trial 2 ($N=14$ of 20 trials, $p=0.115$).

The next set of analyses examined the hypothesized association between social dominance and feeding priority. As revealed in Table 2, socially subordinate males were significantly more likely to monopolize the fruit slice in both Trial 1 ($N=40$ of 53 trials, $p=0.001$) and Trial 2 ($N=42$ of 51 trials, $p=0.001$).

DISCUSSION

Results experimentally demonstrated that neither body size nor scrotal colour contributed to feeding priority outcome. The principal, and perhaps surprising result of this study was that social dominance is inversely predictive of feeding priority. While feeding priority outcomes may be inversely related to social dominance relationships, asymmetries in potential resource holding power (RHP: MAYNARD SMITH, 1982; PARKER, 1974) in traits other than body size, such as strength, may explain these results. Nevertheless, for the present study it is impossible to evaluate for sure which characteristics of RHP can account for these findings. Furthermore, it is not possible at this time to identify what assessment signals or information the monkeys may possess about each other's capabilities.

It also can be argued that differential access to resources can result from differences in motivation or need (i.e. BERNSTEIN, 1981). It appears unlikely that the present results reflect pay-off differences between the males, given that subjects were offered only part of their normal breakfast prior to introductions and were presumably equally motivated to eat. Moreover, there is no *a priori* reason to propose that males of low social dominance should be more motivated to eat.

How might these findings apply to populations of wild vervet monkeys? Despite the artificial introduction of adult males in these experiments, wild vervet monkey males have an opportunity to interact with unfamiliar animals in two contexts. First, during intergroup encounters vervet monkeys often associate with unfamiliar individuals (CHENEY, 1981). Second, males can interact with individuals from neighboring social groups during the process of dispersal from natal groups and, thereafter, when transferring to other groups (CHENEY & SEYFARTH, 1983).

WRANGHAM (1981) found an association between dominance and drinking priority in wild vervet monkeys so the possibility that dominant males, on average, gain greater access to food resources in free-ranging populations cannot be dismissed categorically. In the present investigation, unfamiliar males of relatively the same size, scrotal colour and age were introduced thereby allowing for an assessment of basic rank. These experiments cannot offer the "dependent rank" of individuals, however, and dominance outcomes of these experiments could differ under long-term social group conditions, or under the influence of kinship (KAWAI, 1965).

Furthermore, it may be premature to generalize the finding of an inverse relationship between social dominance and feeding priority to other primates. For example, while no publications to the best of my knowledge have described a direct comparison between these dominance relationships during paired introductions, the relationship between these two dominance assessments is typically consistent in Japanese macaques (IHOBE, pers. comm.). Perhaps this difference between vervet monkeys and Japanese macaques is not surprising. Vervet monkeys and Japanese macaques differ in the means by which they engage in dominance interactions. Japanese macaques frequently supplant competitors to gain access to resources in both captive and wild populations (SOLTIS, pers. comm.), whereas for vervet monkeys, supplantations play but a minor role. By contrast, wild vervet monkeys typically "take turns" when at watering holes, as do captive vervets, when drinking water from spigots or when eating chow (WRANGHAM, 1981; FAIRBANKS, pers. obs.; GERALD, pers. obs.). For vervet monkeys, Feeding

priority experiments may invite a scramble competition, where resources are acquired on a first come first serve basis. Indeed, during the Feeding priority experiments, monkeys did not displace each other to obtain the orange slice; rather, the winner was the male who quickly took and ate the orange slice.

A non-contradictory mechanism for these findings derives from neuro-endocrine evidence, which suggests that relative to males of higher dominance rank, monkeys of low status may exhibit lower concentrations of CSF 5-hydroxyindoleacetic acid (CSF 5-HIAA), the primary serotonin metabolite (see HIGLEY et al., 1996). Impaired serotonergic function has been also linked to impulsivity (HIGLEY et al., 1996; FAIRBANKS et al., 1999). Clearly, the function of CSF 5-HIAA for Japanese macaques and vervet monkeys would be expected to be the same. Nevertheless, given the infrequent occurrence of supplantations in the behavioural repertoire of vervet monkeys, low ranking vervet males could possibly gain food rewards under risky conditions from exploiting their impulsive tendencies.

I propose to consider the acquisition and consumption of resources on a temporal continuum. Male dominance rank may best predict access to resources when there is direct contest competition over a resource, which is not immediately exhaustible (e.g. a shady location or a prime spot in a tree surrounded by fruit). Male dominance rank may not predict access to resources when there is scramble competition for an ephemeral and small resource (e.g. a suddenly appearing invertebrate or the slice of fruit provided in these present experiments). In the latter case, the first come first serve rule may overpower any advantage that dominant males have in a direct contest between individuals. There is no reason to suspect that a past relationship between individuals (dominance) or differences in opponents' power (RHP) should affect the acquisition of ephemeral resources, whereas quick and impulsive tendencies might. The high impulsivity of low ranking males (with low concentrations of CSF 5-HIAA) may give them a competitive edge in such scramble competitions, even though in many other contexts, high ranking males gain priority of resources through direct contests.

While the data here cannot readily offer a mechanism to account for the findings, they do underscore the potential distinction between dominance measures based on agonistic interactions and those based on measures of priority of access to resources. This result should serve as a reminder that differences in dominance relationships may be yielded from different behavioural contexts and operational definitions of dominance.

Acknowledgements. I am grateful to J. MANSON, S. PERRY, N. BLURTON JONES, L. FAIRBANKS, J. DEE HIGLEY, I. BERNSTEIN, and J. SOLTIS for providing me with intellectual stimulation for this study. I thank J. SOLTIS, I. BERNSTEIN, and W. JONES for offering constructive comments on an earlier draft of this paper. I extend my sincere gratitude to J. BAULU for offering me permission to conduct this study at the BPRC and WR and to J. BAULU, C. CURRIE, C. O. SUTTON, G. EVANS, E. THORINGTON, G. GRIFFITH, D. ROLLINS, L. MARSHALL, F. SKINNER, and the Staff at the BPRC and WR for providing me with invaluable logistical support. I also thank the Department of Immigration in Barbados for granting me permission to live in Barbados. The BPRC and WR, a Sigma-Xi, Grant-in-Aid, the Department of Anthropology at UCLA, and the Graduate Division at UCLA generously funded this study. The Animal Research Committee at UCLA approved this research (ARC Number 97-179-01).

REFERENCES

- ALTMANN, J. 1974. Observational study of behavior: sampling methods. *Behaviour*, 49: 227 – 263.
- BERCOVITCH, F. B. 1996. Testicular function and scrotal color in patas monkeys. *J. Zool. London*, 239: 93 – 100.
- BERNSTEIN, I. S. 1981. Dominance: the baby and the bathwater. *Behav. Brain Sci.*, 4: 419 – 457.

- CHENEY, D. L. 1981. Intergroup encounters among free-ranging vervet monkeys. *Folia Primatol.*, 35: 124 – 146.
- CHENEY, D. L.; SEYFARTH, R. M. 1983. Nonrandom dispersal in free-ranging vervet monkeys: social and genetic consequences. *Amer. Naturalist*, 122: 392 – 412.
- FAIRBANKS, L. A.; FONTENOT, M. B.; PHILLIPS-CONROY, J. E.; JOLLY, C. J.; KAPLAN, J. R.; MANN, J. J. 1999. CSF monoamines, age and impulsivity in wild grivet monkeys (*Cercopithecus aethiops aethiops*). *Brain Behav. Evol.*, 53: 305 – 312.
- FEDIGAN, L. M. 1982. *Primate Paradigms: Sex Roles and Social Bonds*. Eden Press, Montreal.
- GERALD, M. S. 2001. Primate colour reveals social status and predicts aggressive outcome. *Anim. Behav.*, 61: 559 – 566.
- GERALD, M. S.; BERNSTEIN, J.; HINKSON, R.; FOSBURY, R. 2001. A formal method for objective assessment of primate color. *Amer. J. Primatol.*, 53: 79 – 85.
- HIGLEY, J. D.; MEHLMAN, P. T.; POLAND, R. E.; TAUB, D. M.; VICKERS, J.; SUOMI, S. J.; LINNOILA, M. 1996. CSF Testosterone and 5-HIAA correlate with different types of aggressive behaviors. *Biol. Psychiatry*, 40: 1067 – 1082.
- KAWAI, M. 1965. On the system of social ranks in a natural troop of Japanese monkey (I): Basic rank and dependent rank, Japanese monkeys. In: *Japanese Monkeys: A Collection of Translations*, ALTMANN, S. A. (ed.), Edmonton, Alberta, pp. 66 – 86.
- MAYNARD SMITH, J. 1982. *Evolution and the Theory of Games*. Cambridge Univ. Press, Cambridge.
- MENDOZA, S. P. 1993. Social conflict on first encounters. In: *Primate Social Conflict*, MASON, W. A.; MENDOZA, S. P. (eds.), SUNY Press, Albany, pp. 85 – 110.
- NOË, R.; DE WAAL, F. B. M.; VAN HOOFF, J. A. R. A. M. 1980. Types of dominance in a chimpanzee colony. *Folia Primatol.*, 34: 90 – 110.
- PARKER, G. A. 1974. Assessment strategy and the evolution of fighting behaviour. *J. Theor. Biol.*, 47: 223 – 243.
- RALEIGH, M. J.; MCGUIRE, M. T. 1989. Female influences on male dominance acquisition in captive vervet monkeys, *Cercopithecus aethiops sabaeus*. *Anim. Behav.*, 38: 59 – 67.
- ROEDER, J. J.; FORNASIERI, I. 1995. Does agonistic dominance imply feeding priority in lemurs: a study in *Eulemur fulvus mayottensis*. *Int. J. Primatol.*, 16: 629 – 642.
- ROWELL, T. E. 1971. Organization of caged groups of *Cercopithecus* monkeys. *Anim. Behav.*, 19: 625 – 645.
- ROWELL, T. E. 1974. The concept of social dominance. *Behav. Biol.*, 11: 131 – 154.
- ROWELL, T. E. 1988. Beyond the one-male group. *Behaviour*, 104: 189 – 201.
- WRANGHAM, R. W. 1981. Drinking competition in vervet monkeys. *Anim. Behav.*, 29: 904 – 910.

— Received: December 12, 2000; Accepted: February 27, 2002

Author's Name and Address: MELISSA S. GERALD, Cayo Santiago, Caribbean Primate Research Center, P. O. Box 906, Punta Santiago, Puerto Rico 00741, U. S. A. e-mail: cayo_santiago@yahoo.com