PATERNITY, MALE SOCIAL RANK, AND SEXUAL BEHAVIOUR

GENERAL DISCUSSION

The papers included in this symposium-volume represent the first fruits of DNA-fingerprinting and DNA analysis based on PCR-amplification, in some cases in addition to protein analysis or antigen reactions. These studies combine data on social dominance and mating behaviour with genetic paternity exclusions. In Table 1, we have summarized the techniques applied in the various studies and the success rates obtained. The rates of excluding all but one candidate, generally were around 90% or higher. The exclusion rate depends in part on the techniques applied and the number of paternal candidates (see Table 1). This high success rate clearly demonstrates the value of these new techniques for socio-biological studies.

Table 1. A summary of paternity studies of different populations.

Species/authors[1]	Techniques	Success rate	Wild/ captive	Mature M/F[2]	Correlations between		
					DR-RS	DR-MS	MS-RS
Mandrillus sphinx DIXSON et al.	DNA f.: Alu I; $(GTG)_5$	33/36	Enclosure	6/12	+	+*	+*
Macaca fascicularis DE RUITER et al.	7 proteins + DNA f.: Hae III; 33.15, 33.6, $(CAC)_n$	33/45 & DNA: 7/7	Wild	10/12 & 1-4/3-5	+	+	0
Macaca arctoides BAUERS et al.[3]	DNA f.	24/24	Captive	1-7/8-16	+	?	?
Macaca sylvanus PAUL et al.	DNA f.: Alu I, Hae III, Hinf I; $(GTG)_5$, $(GA)_8$, $(GT)_8$, $(GATA)_5$, $(GGAT)_4$, $(GACA)_4$	70/75	Enclosure	16-33/75	+	+*	+*
Macaca mulatta SMITH	8 proteins, 11 antigens DNA f.: Hae III, Hinf I, Alu I; 33.6	226/286	Captive	4-18/35	0	?	?
Pan troglodytes SUGIYAMA et al.	PCR: GT dinucleotide repeat (PTGT23)	4/8	Wild	1/8	0**	+	0**
Erythrocebus patas OHSAWA et al.	DNA f.: Hinf I, Hae III; 33.15, myo	12/12	Wild	1-3/2-4?	+?	+?	0
Macaca mulatta BERARD et al.	DNA f.: Hinf I; $(CAC)_n$, $(GATA)_4$, $(GACA)_4$, $(CT)_8$, $(CA)_8$	11/15	Semi-free-ranging	11/18	0	0	0†
Macaca fuscata INOUE et al.	DNA f.: Hinf I, Hae III; myo, YNH24, YNZ22. PCR: GT dinucleotide repeat (MFGT2, MFGT5, MFGT17)	15/17	Captive	9-10/ 18-24	0	+	0

1) In time order of the symposium presentations; 2) number of sexually mature males and females (M/F); 3) not included in this volume. DNA f.: DNA fingerprinting; DR: dominance rank; RS: reproductive success; MS: mating success; +: a positive correlation; 0: no correlation; ?: no definitive conclusions are drawn from the data. *Only copulations during periods of maximum fertility were analyzed; **in one out of four cases the only adult male in the group was excluded; †by BERARD et al. in prep.

To facilitate comparison among species with respect to the correlations between dominance rank, reproductive success, and mating success, we have summarized these relationships in Table 1. In addition we have included under which conditions the animals lived and the numbers of sexually mature males and females in the social groups studied.

As pointed out by DE RUITER and VAN HOOFF (this volume), from the different patterns of correlations between dominance rank, reproductive success, and mating success, aspects of the social system can be inferred. The present collection comprises eight studies. One study by SMITH on *Macaca mulatta* did not yield statistically significant correlations between dominance rank and reproductive success during most of the 15 years of the study (but see below). One study (DE RUITER & VAN HOOFF) on *Macaca fascicularis* demonstrated a positive correlation between dominance rank (alpha status) and reproductive success and between dominance rank and mating success during a female's period of maximum fertility. A recent study of BAUERS and HEARN (in prep.) found a strong (almost exclusive) relationship between alpha male status and reproductive success in a captive population of *Macaca arctoides* studied over an eight-year period, but they did not formally analyze mating success at the time of the symposium.

Two studies (PAUL et al.; DIXSON et al.) did find three positive correlations for *Macaca sylvanus* and *Mandrillus sphinx* respectively. This indicates success by high ranking males due to higher mating success. In these two studies, matings specifically during fertile periods of females were analyzed; in the study by PAUL et al. matings at other times were much more equally distributed and in the study by DIXSON et al. there was mate guarding by top males during the peri-ovulatory phase of the female cycle. The results of the three studies by DIXSON et al., PAUL et al., and DE RUITER and VAN HOOFF, therefore all point towards a rank advantage due to selective mating. Although numbers are low and significant correlations cannot be found, therefore, the studies by SUGIYAMA et al. and OHSAWA et al. also indicate an advantage for high ranking or "resident" males due to high mating success. This is true also for a study of captive chimpanzees by TAKENAKA et al. (1993).

INOUE et al. found a pattern with a positive correlation only between dominance rank and mating success for *Macaca fuscata*. Since neither dominance rank nor mating success determine reproductive success, other factors such as female choice or alternative male strategies are likely to be involved here, a conclusion also drawn by INOUE et al. Also BERARD's study on rhesus monkeys (*Macaca mulatta*) points towards a much more equal distribution of paternity, which he attributes to female choice and male alternative strategies as well. Although, in his study on captive rhesus macaques, SMITH found no positive correlation between rank and reproductive success during most of the single seasons, this correlation was present if he combined data for different seasons. Reproductive success, however, preceded high rank (rather than concurring with it). SMITH concludes that this is an effect of female preference for male qualities which also lead to high rank, later on in the lives of these males. No evidence for such a mechanism is available from studies of wild animals.

As we saw, quite a few studies showed that having high dominance rank plays a role in achieving reproductive success. The reproductive success needs to be not always correlated with a high *global* mating success. Matings of dominant animals may be restricted to the fertile periods (*selective* mating success). In many cases dominant males appear to have exclusive access to females during crucial periods, either through priority of access, or because females have a preference for dominant males or males with characteristics reflecting dominance potential, a preference which is exerted at the moment of greatest fertility.

REFERENCE

TAKENAKA, O., S. KAWAMOTO, T. UDONO, M. ARAKAWA, H. TAKASAKI, & A. TAKENAKA, 1993. Chimpanzee microsatellite PCR primers applied to paternity testing in a captive colony. *Primates*, 34: 363 – 369.

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