Monkeys are superior to men in this: When a monkey looks into the mirror, he sees a monkey.

Malcolm de Chazal, c. 1940

The Monkey in the Mirror

Socio-Cultural Networks in Bonnet Macaques

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Primate Social Complexity

THE INDIVIDUAL

A rich repertoire of communicative behaviours to facilitate individual expression and develop complex social relationships

THE SOCIETY

Complex groups with individuals of different ages, sexes, dominance ranks and kinship

Development of sub-groups, temporary alliances and long-term relationships that cut across these categories

Complex network of associations and interactions with many alternative strategies for survival and reproduction

Long-lived social groups in which individuals can pursue a number of different strategies during their lifetimes

Inheritance Systems

Basic genetic inheritance system

- Involves acquisition, storage and transfer of genetic elements
- Variation random and independent of environment or developmental history of organism
- Subject to neo-darwinian individual selection by environment

Evolved lamarckian inheritance systems

- Involve acquisition, storage and transfer of information
- Variation generated by organism-environment interactions
- Subject to natural individual and/or group selection
- Inheritance of acquired characters possible

Behavioural Inheritance Systems

 Information – usually patterns of behaviour – acquired by accident or individual learning during interactions with the ecological and social environment, and stored in the nervous system

 Such information transmitted by social learning between individuals within and across generations

Inheritance at the level of the organism – generation of individuality

Behavioural Inheritance in Primate Societies

Three issues in behavioural inheritance that impact strongly on primate social structure and dynamics

Phenotypic flexibility in social behaviour

Individual behavioural traits and social traditions

Stable traditions and cultural selection



The Bonnet Macaque Macaca radiata

- Endemic to peninsular India
- Wide ecological distribution: montane evergreen forests, moist and dry deciduous forests, bamboo forests, dry scrub jungles, and human habitations
- Multifemale, usually multimale, troops of 5-75 individuals
- Females generally philopatric, with linear dominance hierarchies and close social relationships
- Emigration of juvenile and adult males from their natal troops common, but not invariable
- Unstable dominance hierarchies among adult males through aggression and coalitions; unusually extensive affiliative relationships between males
- Society typically promiscuous with periodic consortships, ample mating opportunities, mutual tolerance among males and subtle female mate choice





Study Areas and Troops, Methods

Study areas and troops

Two troops: University of Agricultural Sciences, Bangalore; 1993-1996

Seven troops: Mudumalai Wildlife Sanctuary, Tamil Nadu; 1996-1997, 2000-present

Two troops: Bannerghata National Park, Karnataka; 2000-2001

Fourteen troops: Bandipur National Park, Karnataka; 2000-present

Principal methods

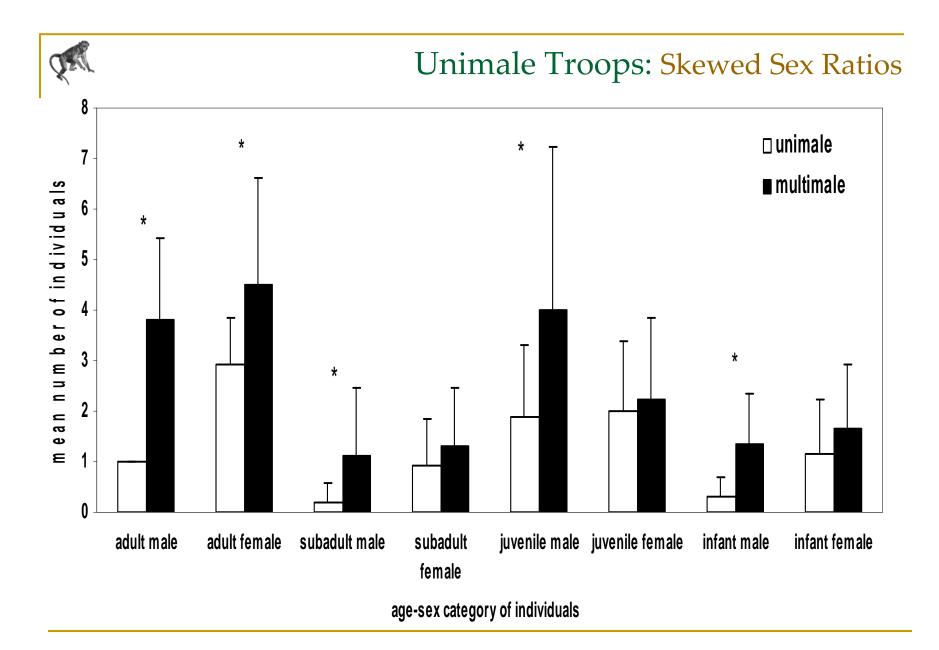
Identification of social groups and individuals

Enumeration of demographic variables

Sampling of behaviours: *ad libitum* observations, focal animal sampling, and opportunistic sequence sampling



- 11 out of 21 troops (~52 %) in the Bandipur-Mudumalai forests with a unique unimale social organisation
- Unimale troops never reported earlier from these populations; present in very low proportions in other populations (~13-14 %)
- Stable groups with adult sex ratio of 1 to 0.25 each troop with a single adult male and 1 to 4 adult females
- Total group size (11 ± 3 individuals) significantly smaller than that of multimale troops (20 ± 9 individuals)
- Unimale troops found only in forested tracts, multimale groups in both forests and around human habitations





Unimale Troops: Demography

 Unimale troops remarkably depleted in males of all age categories – subadult, juvenile and infant

 Total number of individuals and females in these age categories, however, not different between unimale and multimale troops

 Male depletion in unimale troops from other populations: Data on Mysore and Kolar populations – from Kurup 1981



Significant female-biased birth sex ratio (1:4) in unimale troops in contrast to that (1:1) in multimale troops

Infanticide?

- Virtually identical birth rates in the two populations
- No observational evidence for any directed aggression

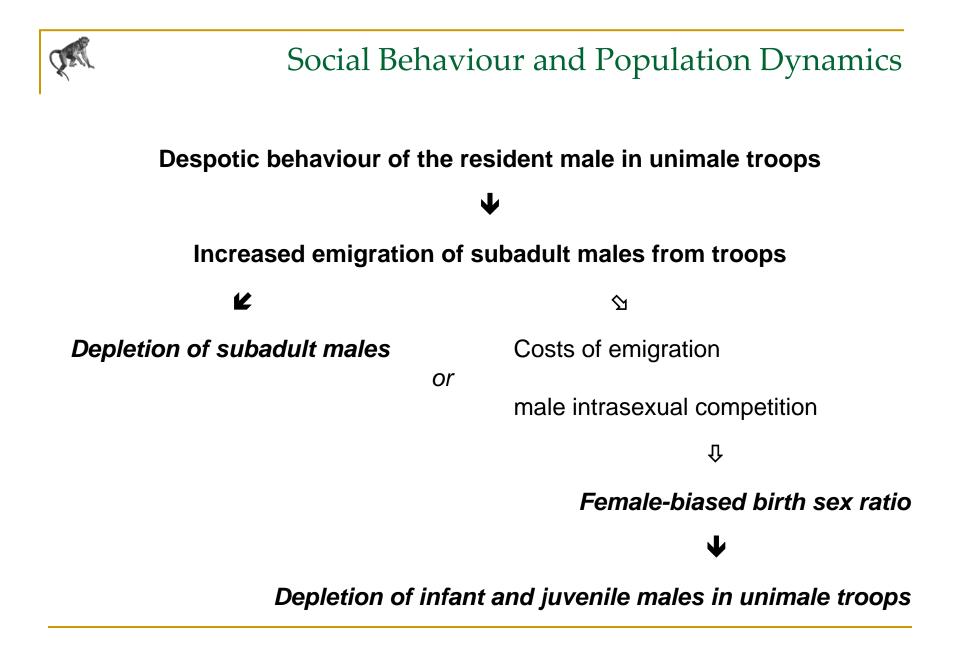
Facultative skewing of birth sex ratio dependent on the nature of the social organisation

- Documented for the first time in any species!
- Proximate mechanisms presently unknown
- Ultimate factors behavioural mechanisms?



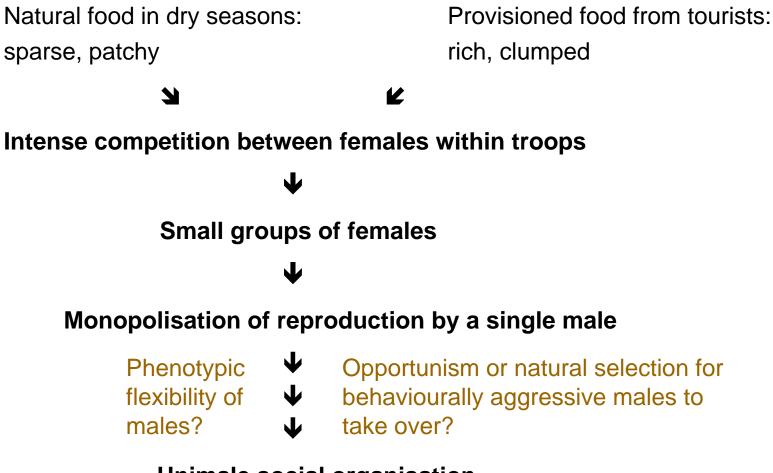
Unimale troops as harems!

- Reproductive monopolisation by the resident adult male unlike the tolerant males of multimale troops
- Severe aggression towards subadult and juvenile males rare in multimale groups
- Active herding of females by the resident male virtually unknown in multimale troops except during consortships
- Aggressive troop defense by the adult male, often with injuries to the challenging males – no participation of the alpha male of multimale groups in any inter-troop encounter
- Active prevention by the resident male of immigration by new males into the troop – not usually observed in multimale groups
- Emigration of females never observed in other populations





Evolution of Unimale Troops: A Model



Unimale social organisation

Phenotypic Flexibility

- Context-dependent phenotypic transformations in behaviour in response to variations in ecological and social environments
- Occurrence of transformations within a single individual an advantage in terms of individual fitness
- Observed in individuals living in rapidly changing environments with continuous, but reversible, fluctuations
- Such transformations, therefore, often reversible
- Integration of behavioural flexibility into the life-histories of individuals
- Integrated behavioural variability often subject to natural selection



Phenotypic Flexibility among Bonnet Macaques

Unpredictability in food abundanceand distribution $\Rightarrow \Rightarrow \Rightarrow$

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Flexibility in female social strategies dependent on their dominance rank

Flexibility in male behavioural strategies towards females and other males in groups with varying female number

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Flexibility in female emigration strategies

Smaller female group sizes in some habitats

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Skewing of sex ratio of offspring by males or females in different groups

Individual Behavioural Traits and Social Traditions

- Individual behavioural traits produced by accident or individual learning give rise to behavioural traditions through social learning
- This process serves in the generation of individuality and leads to increase in behavioural variation within the group
- Traditions are deduced from spatial, temporal or social patterns of behavioural variation not consistent with genetic or environmental determination or individual learning
- Three types of behavioural patterns in traditions:

Rapid-spread patterns through a segment of the population indicating largely horizontal, within-generation transmission

Parent-offspring patterns of similarity in novel behaviours indicating vertical withinlineage transmission

Stable group-specific patterns unexplained by genetic differences, shared environments or by demographic traits of the groups – usually indicating vertical, horizontal and oblique transmission



Behavioural Traditions in Bonnet Macaques: Types

Rapid-spread patterns

Mango-washing:	Two subadult males in Mudumalai BM21
Bipedal begging:	Two adult males and one adult female in Bandipur BM4
Car-raiding:	Two adult males and one subadult male in Bandipur BM11
Male-adoption:	Three juvenile males and one juvenile female in Bandipur BM5
Tool use manufacture:	One adult female in Bangalore GK1

Parent-offspring patterns

Coo call-begging:A mother-daughter pair in Bangalore GK1; two adult females in BM5Interaction with humans:A mother-two daughters-two sons in Bangalore GK1Allogrooming patterns:Adult females in Bangalore GK2

Group-specific patterns

Foraging style:	Most individuals in Bangalore GK1 and Bangalore GK2
Branch-shaking:	Six adult females in Bangalore GK2
Allogrooming patterns:	Adult females in Bangalore GK2



Behavioural Traditions in Bonnet Macaques: Variation

Troop	Troop	Rapid spread of novel behaviour				Parent-offspring similarity		Group-specific behaviour			
	size I	Т	П	ш	IV	v	VI	VII	VIII	іх	х
	Population I										
BM1	32.2										
BM2	19.3										
BM3	4.9										
BM4	15.5										
BM5	15.9										
BM6	31.9										
BM7	13.6										
BM8	6.8										
BM9	20.5										
BM10	9.8										
BM11	9.7										
BM12	20.6										
BM13	7.4										
BM14	6.3										
BM15	27.0										
BM16	28.6										
BM17	26.3										
BM18	12.6										
BM19	9.8										
BM20	15.8										
BM21	5.0										
	Population II										
GK1	48.0										

32.5

GK2





Stable Traditions and Cultural Selection

A stable social tradition in bonnet macaques and other macaques:

Cultural inheritance of dominance rank among adult females

- Daughters occupy ranks just below those of their mothers
- Older sisters occupy ranks just below their younger sisters
- Entire matrilines rise above other matrilines during rare changes in the dominance hierarchy
- Females depend on support from other dominant individuals for the acquisition and maintenance of their ranks

Amongst bonnet macaque males:

- Dominance ranks depend on general competitive abilities, physical body condition, manipulative skills and perhaps, a suitable temperament
- Such traits may be under direct genetic control selected for by natural selection



Affiliative Networks in Bonnet Macaques I

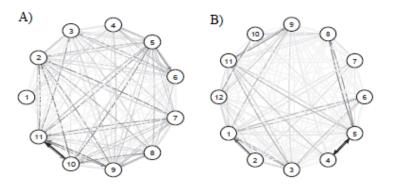
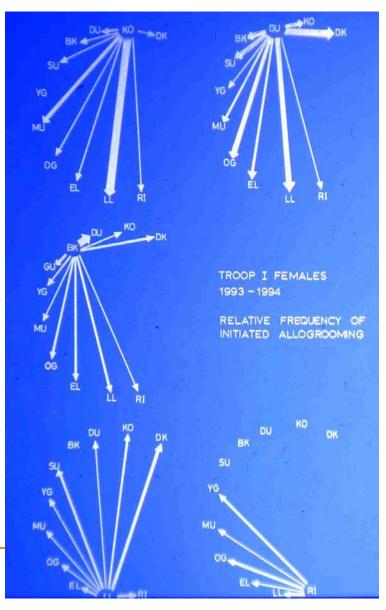


FIG. 1: The social network of (a) female and (b) male members of the bonnet macaque troop, where the interaction strength between each pair of individuals is determined by their corresponding grooming frequency (GF).





Affiliative Networks in Bonnet Macaques II

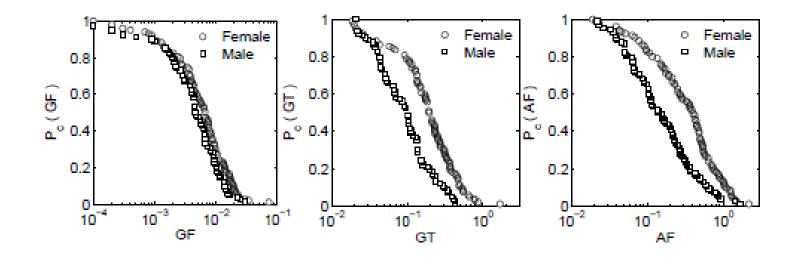


FIG. 2: The distribution of interaction strengths, defined in terms of (a) grooming frequency (GF), (b) grooming time (GT), and (c) approach frequency (AF), for both the female and male macaque social networks. The data indicates an exponential nature for all three distribution.



Affiliative Networks in Bonnet Macaques III

TABLE I: Modular decomposition of the male and female bonnet macaque social networks, indicating the membership of individuals in different modules. Each individual is indicated by a number that corresponds to its rank in the linear dominance hierarchy, with '1' corresponding to the most dominant. The number of communities obtained is indicated by m, whereas the maximum modularity of the empirical network and the corresponding randomized network is represented by Q and Q_{rand} respectively.

Gender	Type	Q	m	Q_{rand}	Modular identity			
Female	\mathbf{GF}	0.121	2	$0.081 {\pm} 0.017$	$(1\ 2\ 3\ 4\ 5\ 10)\ (6\ 7\ 8\ 9\ 11)$			
	\mathbf{GT}	0.140	2	$0.098 {\pm} 0.021$	$(1\ 2\ 3\ 4\ 5\ 10)\ (6\ 7\ 8\ 9\ 11)$			
	\mathbf{AF}	0.110	2	$0.073 {\pm} 0.020$	$(1\ 2\ 3\ 4\ 5\ 10)\ (6\ 7\ 8\ 9\ 11)$			
Male	\mathbf{GF}	0.085	2	$0.130 {\pm} 0.025$	$(1\ 2\ 3\ 4\ 9\ 12)\ (5\ 6\ 7\ 8\ 10\ 11)$			
	\mathbf{GT}	0.165	4	$0.137 {\pm} 0.024$	$(1 \ 2 \ 3) \ (4 \ 5) \ (6 \ 8 \ 10) \ (7 \ 9 \ 11 \ 12)$			
	\mathbf{AF}	0.240	4	$0.143 {\pm} 0.025$	$(1\ 2\ 3\ 6\ 7)\ (4\ 5\ 8)\ (9\ 11)\ (10\ 12)$			



No genetic or physiological determinants of dominance rank among female macaques

Physiological and behavioural traits strongly correlated to dominance ranks:

- Higher levels of stress and abortion among higher-ranked females
- Ability to facultatively skew sex of offspring towards daughters by highranked and towards sons by low-ranked females
- Adoption of different social strategies according to rank of actor and that of target individual

Epigenetic or cultural selection for these traits?



Gene-Culture Coevolution

Behavioural and life-history characteristics of bonnet macaques that may facilitate establishment of social traditions and play a role in gene-culture coevolution in this species

- Stable matrilineal social structures
- Relatively long period of juvenile dependence that may promote behavioural transmission during maternal care
- Relatively long post-menopausal life of females that may allow transfer of environmental information across generations to increase fitness of offspring and relatives

Old females and males lead troop movements in GKVK and Bandipur

• A genetic polymorphism at 5-HTTLPR could be responsible for intraspecific variability and flexibility in bonnet macaque behaviour



- Behavioural plasticity capacity to evolve variable social organisations and individual behavioural strategies
- Remarkable success of the species in all environments:
- Genetic and behavioural predispositions to evolve significant variability in life-history strategies within different socioecological networks and, in turn, modify them in different ways
- Ecological success second only to humans amongst primates in geographical distribution

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