



Genes code for proteins, not monkeys.

Inspired by Patrick Bateson, 2003





The Monkey in the Mirror!

Social and Cultural Evolution in a Primate Society

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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**
-

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

Primate Evolutionary Biology: Approaches

Individuals within populations

- Ontogeny – birth patterns and developmental profiles
- Biography – behavioural flexibility and reproductive strategies

Populations within species

- Demographic profiles in space – latitudinal studies
- Population histories in time – longitudinal studies

Species within evolutionary lineages

- Cross-species comparisons and evolutionary patterns
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Behavioural Inheritance in Primate Societies

Four 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
 - Social learning and evolution of complex cognition
-

Behavioural Inheritance in Primate Societies

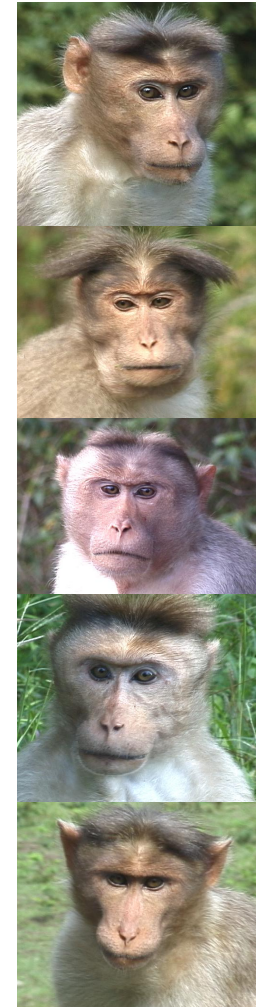
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The Bonnet Macaque *Macaca radiata*

- Multifemale, usually multimale, troops of 5-75 individuals
- Females generally philopatric, with strong linear dominance hierarchies
- Emigration of juvenile and adult males from their natal troops common, but not invariable; immigration permanent or transient
- Unstable dominance hierarchies among adult males through aggression and coalitions; unusually extensive affiliative interactions 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

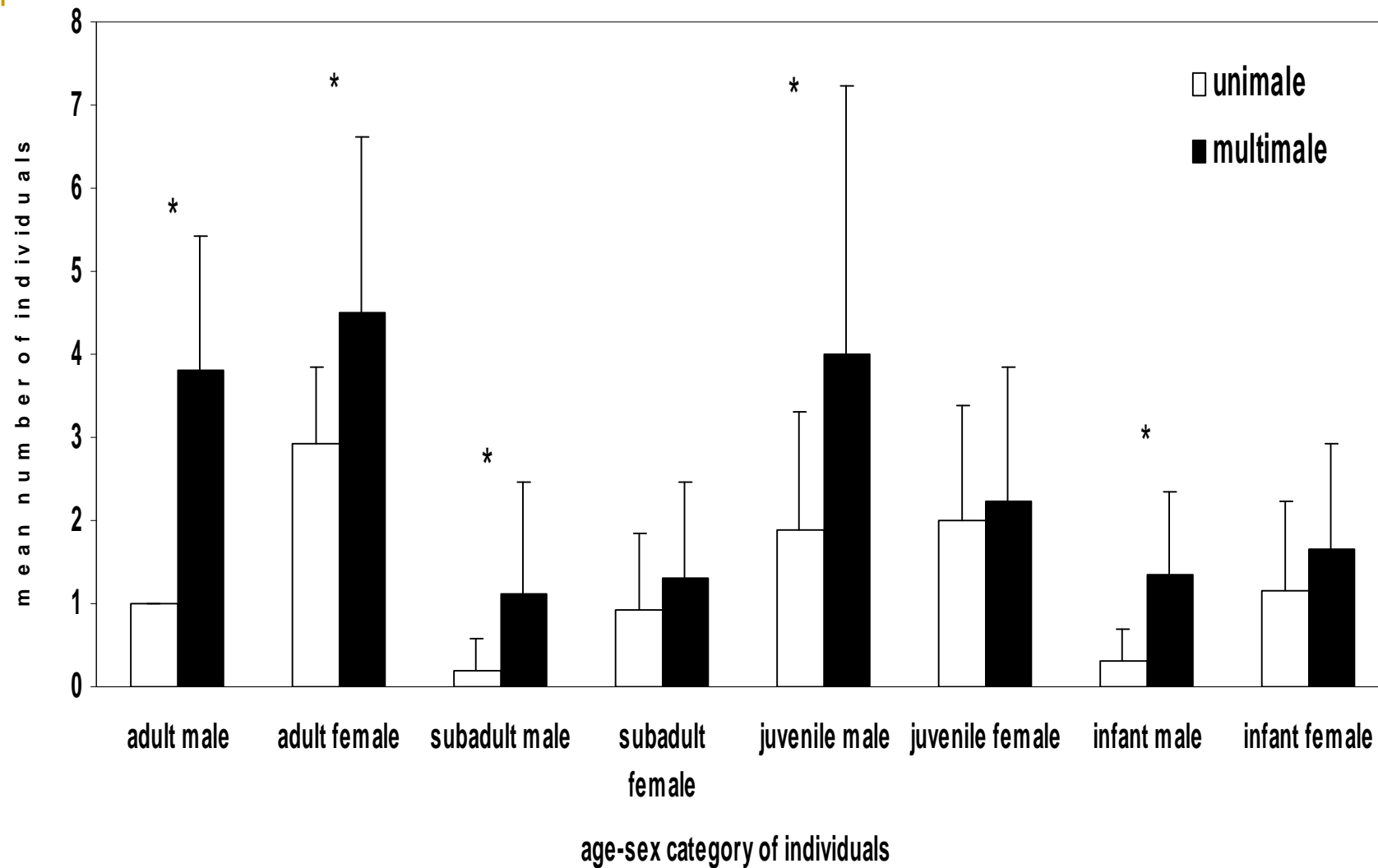


Unimale Troops in Bonnet Macaques

- 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: Skewed Sex Ratios



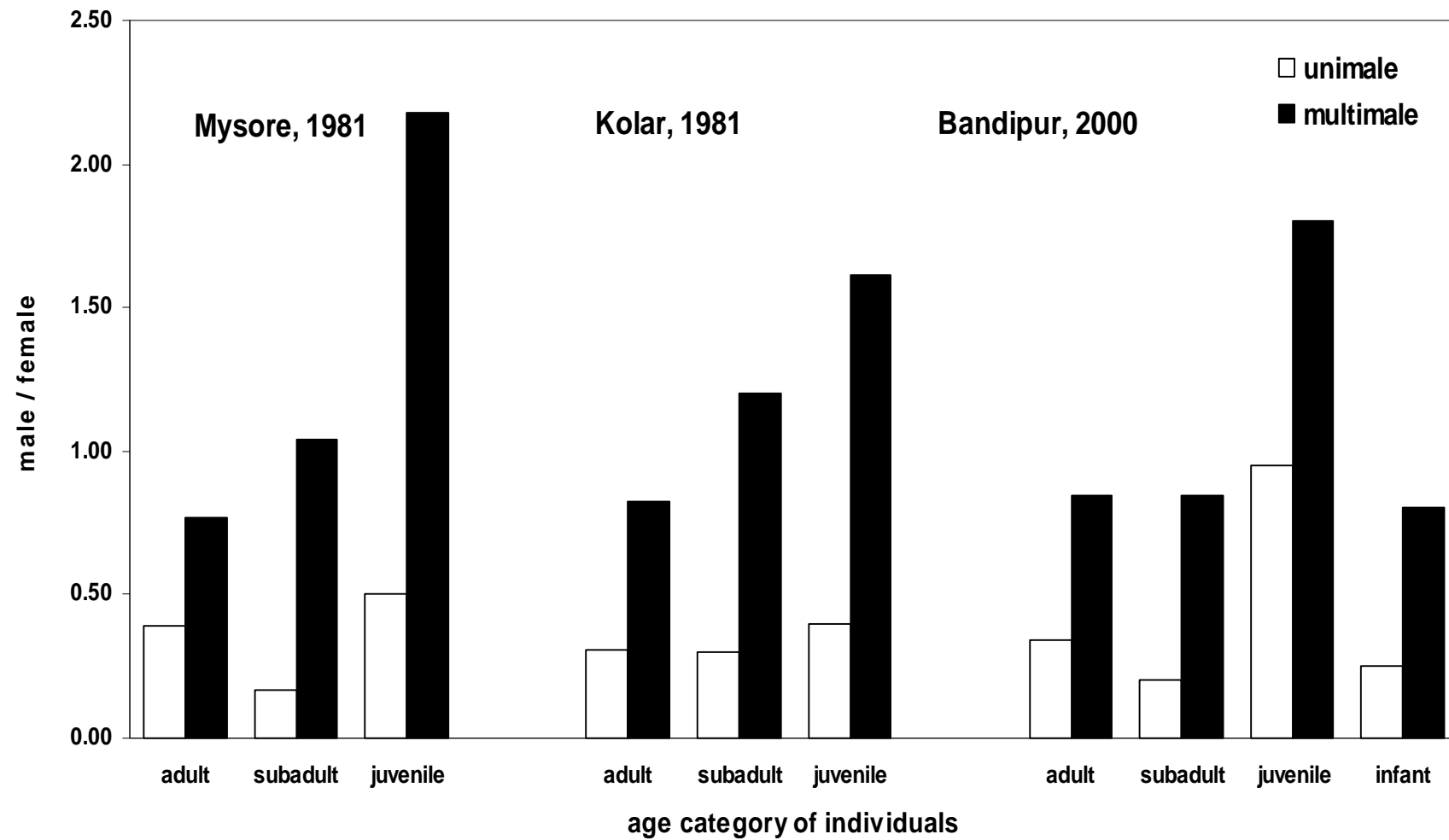


Unimale Troops: Demography

- 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



Skewed Sex Ratios in Other Unimale Troops





Unimale Troops: Biased Birth Sex Ratio

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: Novel Behaviour

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



Social Behaviour and Population Dynamics

Despotic behaviour of the resident male in unimale troops

⇒

Increased emigration of subadult males from troops

↓

Depletion of subadult males

∅

Costs of emigration
or
male intrasexual competition

⇒

Female-biased birth sex ratio

⇒

Depletion of infant and juvenile males in unimale troops



Evolution of Unimale Troops: A Model

Natural food in dry seasons:
sparse, patchy

Provisioned food from tourists:
rich, clumped

↑

↑

Intense competition between females within troops

⇒

Small groups of females

⇒

Monopolisation of reproduction by a single male

Phenotypic
flexibility of
males?

⇒
⇒
⇒

Opportunism or natural selection for
behaviourally aggressive males to
take over?

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 abundance
and distribution

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ò ò ò

Smaller female group sizes
in some habitats

Flexibility in female social strategies
dependent on their dominance rank

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

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

Flexibility in female emigration strategies

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 within-lineage 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 BM5
- Interaction with humans:** A mother-two daughters-two sons in Bangalore GK1
- Allogrooming patterns:** Adult females in Bangalore GK2

Group-specific patterns

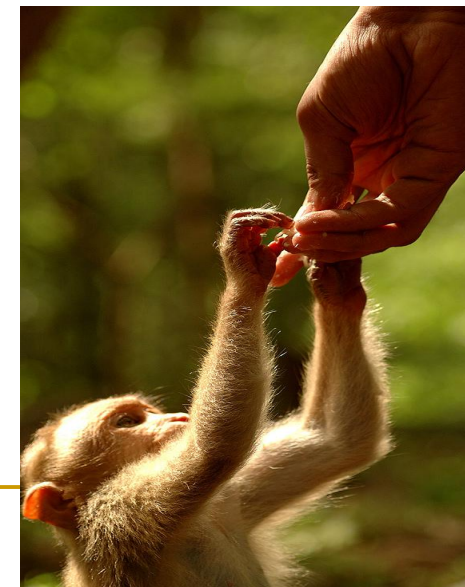
- Foraging style:** Most individuals in Bangalore GK1 and Bangalore GK2
 - Branch-shaking:** Six adult females in Bangalore GK2
 - Allogrooming patterns:** Adult females in Bangalore GK2
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Behavioural Traditions in Bonnet Macaques: Variation

Troop	Troop size	Rapid spread of novel behaviour					Parent-offspring similarity		Group-specific behaviour		
		I	II	III	IV	V	VI	VII	VIII	IX	X
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					■	■	■	■		
GK2	32.5								■	■	■





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 matriline rises 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

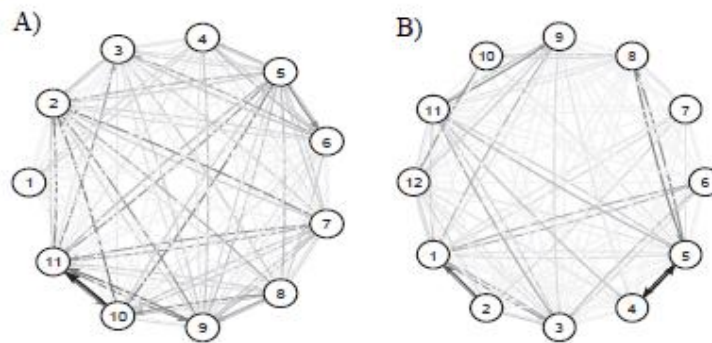
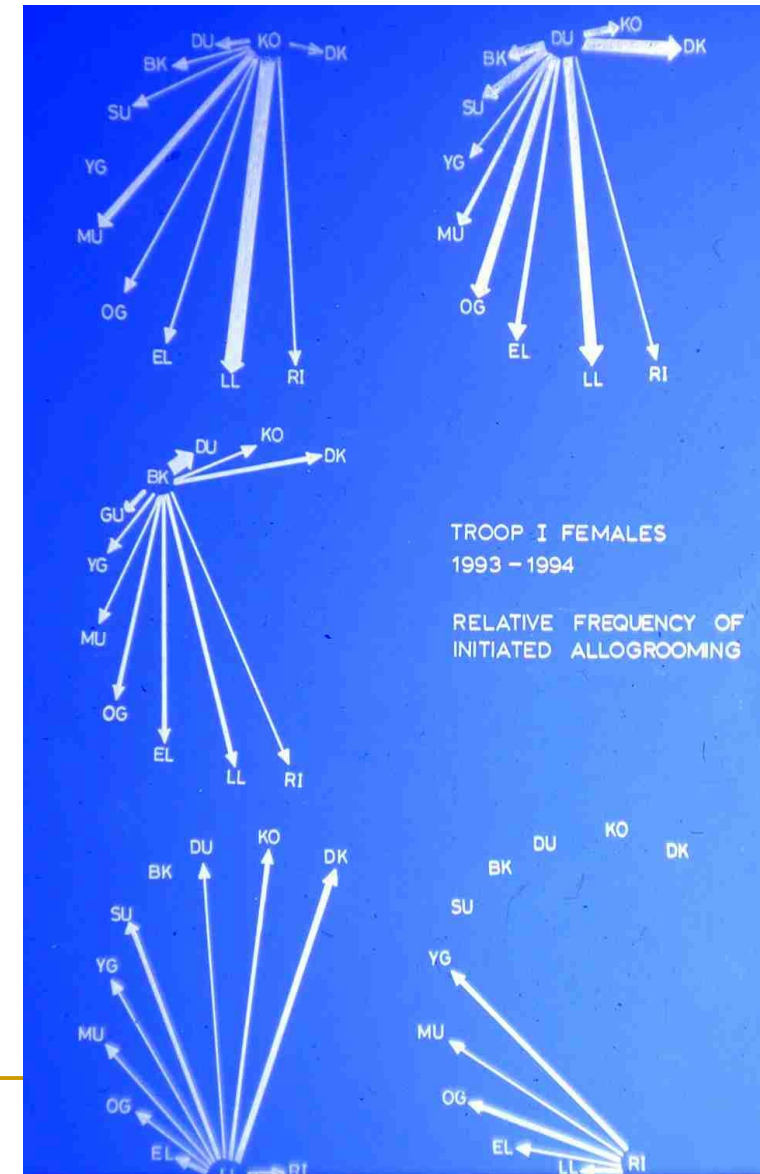


FIG. 1: The social network of (a) female and (b) male members of the bonnet macaque troop, where the interaction strength between each pair of individuals is determined by their corresponding grooming frequency (GF).





Affiliative Networks in Bonnet Macaques II

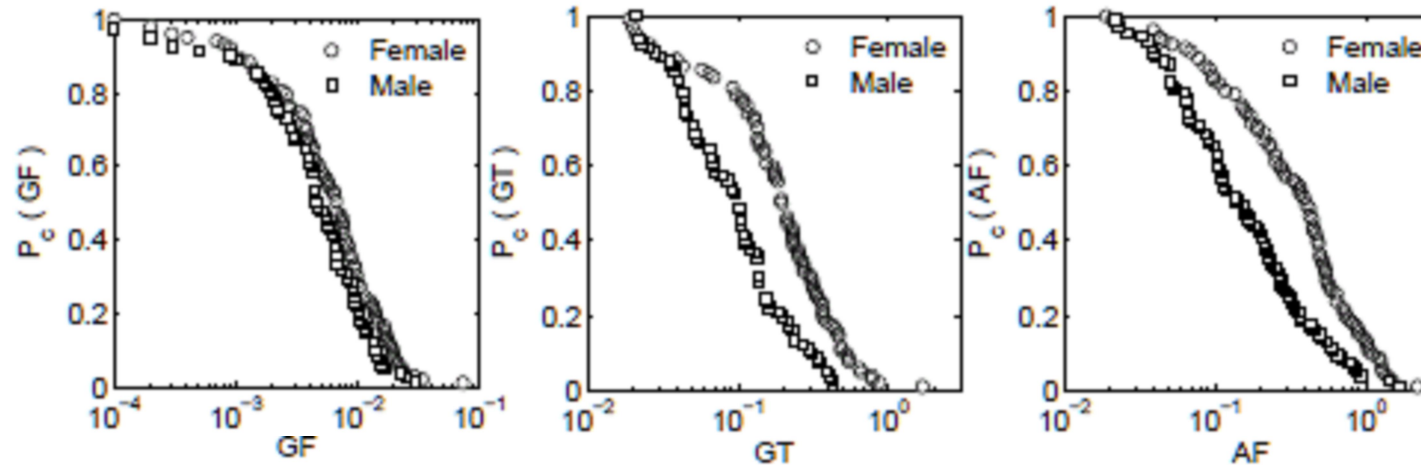


FIG. 2: The distribution of interaction strengths, defined in terms of (a) grooming frequency (GF), (b) grooming time (GT), and (c) approach frequency (AF), for both the female and male macaque social networks. The data indicates an exponential nature for all three distribution.



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	GF	0.121	2	0.081 ± 0.017	(1 2 3 4 5 10) (6 7 8 9 11)
	GT	0.140	2	0.098 ± 0.021	(1 2 3 4 5 10) (6 7 8 9 11)
	AF	0.110	2	0.073 ± 0.020	(1 2 3 4 5 10) (6 7 8 9 11)
Male	GF	0.085	2	0.130 ± 0.025	(1 2 3 4 9 12) (5 6 7 8 10 11)
	GT	0.165	4	0.137 ± 0.024	(1 2 3) (4 5) (6 8 10) (7 9 11 12)
	AF	0.240	4	0.143 ± 0.025	(1 2 3 6 7) (4 5 8) (9 11) (10 12)



Cultural Selection in Bonnet Macaques?

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 high-ranked 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 rôle 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

- Remarkable success of the species in all environments: genetic and behavioural predisposition to evolve significant variability in life-history strategies in different ecological settings

“Instructive (or ‘lamarckian’) inheritance systems are all adaptations that have evolved through darwinian natural selection, often through the selection of randomly generated variations. Once present, these systems constrain and channel evolution. Unlike other constraints on evolutionary change, such constraints do not merely define the range of the possible, they also, more positively, specify what is likely.

The future may spring more directly from the present than we have been accustomed to believe”.

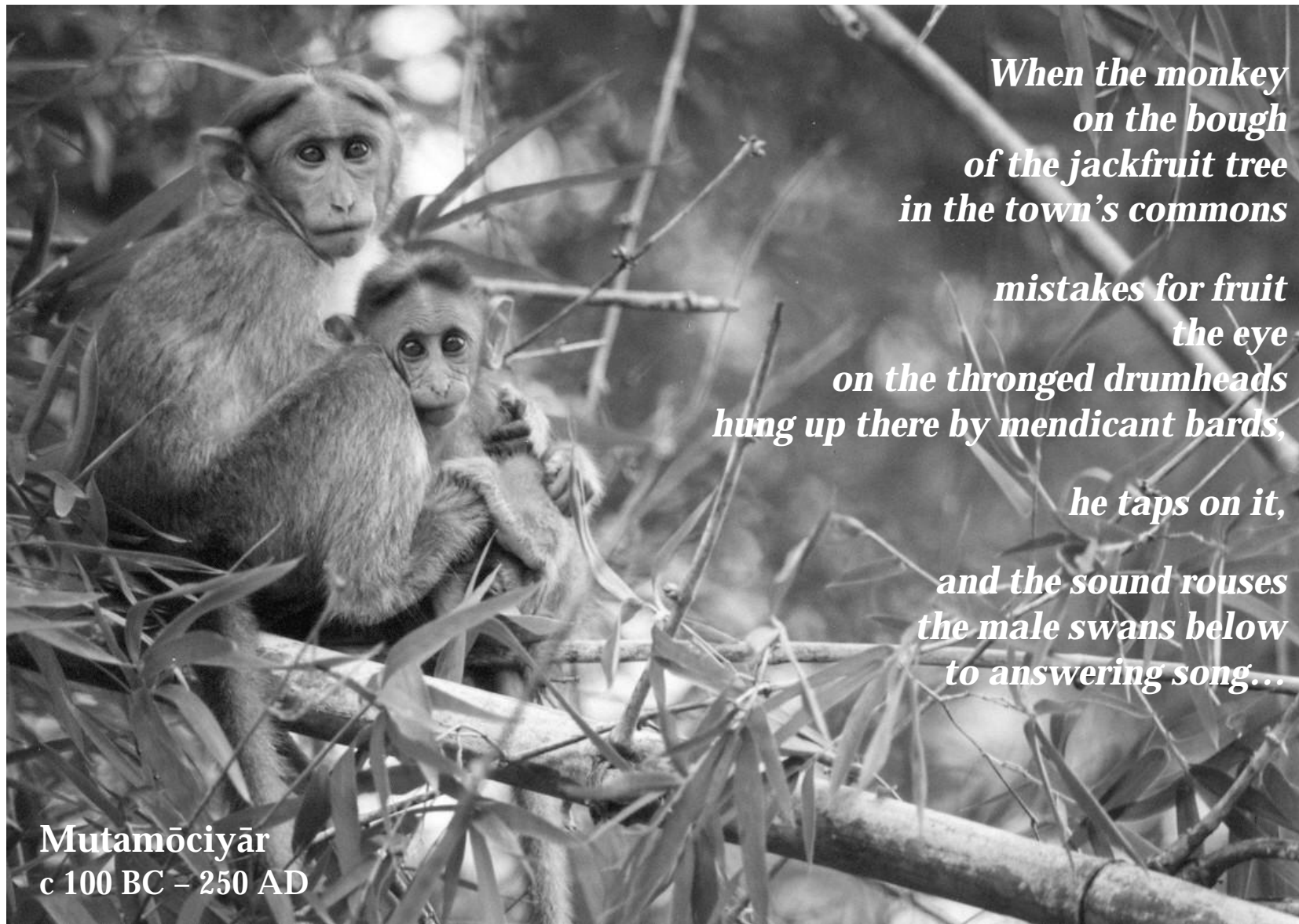
Jablonka, Lamb and Avital 1998

A black and white photograph of a forest path. The path is dirt and leads into a dense forest. Several people are walking along the path. The trees are tall and have thick canopies. The lighting is dappled, suggesting sunlight filtering through the leaves.

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*When the monkey
on the bough
of the jackfruit tree
in the town's commons*

*mistakes for fruit
the eye
on the thronged drumheads
hung up there by mendicant bards,*

*he taps on it,
and the sound rouses
the male swans below
to answering song...*

Mutamōciyār
c 100 BC – 250 AD