TABLE OF CONTENTS

List of tables viii
List of figures x

Synopsis 1

Chapter 1  Introduction 9
1.1 Macaque distribution 10
   1.1.1 Macaque radiation and dispersal 10
   1.1.2 Inter-specific competition 11
   1.1.3 Human influence 11
1.2 Macaque ecology 12
1.3 Macaque societies 12
1.4 Macaque associations 13
1.5 Macaques in India 15
1.6 Aims of study 17
1.7 Study design 18

Chapter 2  Distribution of bonnet macaques, rhesus macaques and their mixed-species troops in peninsular India 21
2.1. Introduction 22
2.2 Aims and objectives of the study 24
2.3 Methods 24
2.4 Results 26
   2.4.1 Distribution limits of the two species 26
   2.4.2 Introduced macaque populations 30
   2.4.3 Overlap in the distribution of the two species 31
   2.4.4 Mixed-species troops 31
2.5 Discussion 34

Chapter 3  Comparative demography of rhesus and bonnet macaques in peninsular India 38
3.1 Introduction 39
3.2 Aims and objectives of the study 40
3.3 Methods 40
Chapter 4  
Social behaviour of a pure-species troop of bonnet macaques

4.1 Introduction
4.1.1 Nepotistic and egalitarian species
4.1.2 Effect of dominance rank and kinship on social relationships between adult females

4.2 Aims and objectives of the study

4.3 Methods
4.3.1 Study area
4.3.2 The study troop
4.3.3 Behaviours observed
4.3.4 Data collection
4.3.5 Sampling effort
4.3.6 Data analysis

4.4 Results
4.4.1 General pattern of affiliative and agonistic behaviour
4.4.2 Relationship between affiliative behaviours and dominance rank
4.4.3 Relationship between agonistic behaviours and dominance rank
4.4.4 Relationship between affiliative and agonistic behaviours
4.4.5 Behavioural correlations across dominant and subordinate females
4.4.6 Idiosyncratic behaviours

4.5 Discussion
4.5.1 Behavioural pattern among adult female
4.5.2 Dominance rank and affiliative behaviour
4.5.3 Dominance rank and agonistic behaviour
4.5.4 Relationship between affiliation and aggression
4.5.5 Individual behavioural profiles
### Chapter 5  Social behaviour of a pure-species troop of rhesus macaques

5.1 Introduction 83
   5.1.1 Ecological distribution 83
   5.1.2 Social organization 83
   5.1.3 Dominance hierarchies 85
   5.1.4 Social relationships 85

5.2 Aims and objectives of the study 87

5.3 Methods 87
   5.3.1 Study area 87
   5.3.2 The study troop 88
   5.3.3 Behaviours observed 89
   5.3.4 Data collection 91
   5.3.5 Data analysis 92

5.4 Results 92
   5.4.1 General behavioural pattern: Affiliative behaviours 93
   5.4.2 General behavioural pattern: Agonistic behaviours 94
   5.4.3 Relationship between affiliative behaviours and dominance rank 94
   5.4.4 Relationship between agonistic behaviours and dominance rank 104
   5.4.5 Relationship between affiliative and agonistic behaviours 107

5.5 Discussion 110
   5.5.1 General pattern of affiliative and agonistic behaviours 110
   5.5.2 Relationship between dominance ranks and affiliative behaviour 112
   5.5.3 Relationship between dominance ranks and aggressive behaviour 113
   5.5.4 Relationship between affiliation and aggression 113
   5.5.5 Comparing rhesus and bonnet macaques 114

### Chapter 6  Social behaviour of mixed-species troops of bonnet and rhesus macaques

6.1 Introductions 118
   6.1.1 Why form mixed-species associations? 118
   6.1.2 Types of mixed-species troops and their behavioural interactions 119
   6.1.3 Mixed-species associations in macaques 121

6.2 Aims and objectives of the study 121
### 6.3 Methods

- **6.3.1 Study area**
- **6.3.2 Study troops**
- **6.3.3 Behaviours observed**
- **6.3.4 Data collection**
- **6.3.5 Data analysis**

### 6.4 Results

- **6.4.1 General behavioural patterns: Affiliative behaviours**
- **6.4.2 General behavioural patterns: Agonistic behaviours**
- **6.4.3 Dominance rank and affiliative behaviours**
- **6.4.4 Dominance rank and agonistic behaviours**
- **6.4.5 Relationship between affiliative and agonistic behaviours**
- **6.4.6 Relationships between the adult female bonnet and rhesus macaques**

### 6.5 Discussion

- **6.5.1 General behavioural patterns: Affiliative and agonistic behaviours**
- **6.5.2 Dominance rank and affiliation**
- **6.5.3 Dominance rank and aggression**
- **6.5.4 Correlation between affiliative and agonistic behaviours**
- **6.5.5 Relationships between the adult female bonnet and rhesus macaques**

### Chapter 7 Mixed-species and pure species troops of bonnet and rhesus macaques: A comparison

- **7.1 Introduction**
- **7.1.1 Comparative studies in social behaviour**
- **7.1.2 How species respond to mixed-species associations: Behavioural changes**
- **7.1.3 Social relationships in bonnet and rhesus macaques**
- **7.2 Aims and objectives of the study**
- **7.3 Methods**
- **7.3.1 Study area**
- **7.3.2 Study species and troops**
- **7.3.3 Behaviours observed**
- **7.3.4 Data collection**
- **7.3.5 Data analysis**
- **7.4 Results**
- **7.4.1 Social organization**
7.4.2 Differences in social behaviour of the two species in pure and mixed troops

7.4.3 Bonnet macaques

7.4.4 Rhesus macaques

7.4.5 Behavioural profiles of female rhesus macaques in the mixed-species troops

7.4.6 Behavioural profiles of female bonnet macaques in the mixed-species troops

7.4.7 Differences in the behavioural profiles of the two species in the mixed troops

7.4.8 Is the behaviour of bonnet macaques in the mixed troops affected by the extra-species individual or by the ecology of the troop?

7.4.9 Do bonnet macaque females behave differently towards the lowest-ranked member of their own species and that of another species?

7.4.10 Do the lowest-ranked bonnet macaque and the last-ranked rhesus macaque behave differently towards the other members of the troop

7.4.11 Changes in communication patterns: Food and alarm calls

7.5 Discussion

7.5.1 Social organisation

7.5.2 Behavioural patterns

7.5.3 Behavioural changes

7.5.4 Interspecific communication

7.5.5 The importance of ecology in determining behaviour

Chapter 8 Concluding remarks

8.1 Changing distributions

8.1.1 Whither bonnet macaques?

8.1.2 Monkeys of a feather?

8.2 Differing demographies

8.3 Patterns of behaviour

8.3.1 Female bonnet macaques

8.3.2 Female rhesus macaques

8.3.3 An uneasy alliance?

8.4 The way ahead!

Bibliography