
Contents

1 Dogs in historical perspective, and conceptual issues of the study of their behaviour	1
1.1 Introduction	1
1.2 From behaviourism to cognitive ethology	2
1.2.1 Dog heroes visit the laboratory	3
1.2.2 Dogs in the comparative psychology laboratory	4
1.2.3 Naturalistic experiments	5
1.2.4 Time for comparisons	7
1.2.5 The cognitive revolution hits dogs	8
1.3 Tinbergen's legacy: four questions plus one	8
1.3.1 Description of behaviour	8
1.3.2 The first question: function	10
1.3.3 The second question: mechanism	10
1.3.4 The third question: development	10
1.3.5 The fourth question: evolution	11
1.4 Evolutionary considerations	11
1.5 What is it like to be a dog?	15
1.6 Lupomorphism or babymorphism?	16
1.7 Modelling of behaviour	17
1.7.1 Top down or bottom up	18
1.7.2 Canon of parsimony	18
1.7.3 Associanism and mentalism	19
1.7.4 Comparing content and operation	19
1.7.5 Comparing intelligence	21
1.7.6 Epigenesis, socialization and enculturation	22
1.8 An ethocognitive mental model for the dog	22
1.9 Conclusions for the future	24
Further reading	26
2 Methodological issues in the behavioural study of the dog	27
2.1 Introduction	27
2.2 Finding phenomena and collecting data	27
2.2.1 Qualitative description	28
2.2.2 Quantitative description	28
2.3 Making behavioural comparisons	30
2.3.1 Wolves and dogs	30
2.3.2 The comparison of breeds	33
2.3.3 Dogs and children	34

2.4 Sampling and the problem of single cases ($N = 1$)	35
2.5 A procedural problem in naturalistic observations: the presence of humans	37
2.6 How to measure dog behaviour?	38
2.7 Asking questions	43
2.8 Conclusions for the future	45
Further reading	45
3 Dogs in anthropogenic environments: society and family	47
3.1 Introduction	47
3.2 Dogs in human society	47
3.3 Interactions between dogs and people in public	51
3.4 Dogs in the family	53
3.5 Dogs at work	56
3.6 Social roles of dogs in human groups	56
3.7 Social competition in dog-human groups and their consequences	57
3.7.1 Aggression and the human family	58
3.7.2 Studying the 'biting dog' phenomenon	58
3.7.3 Identifying risks	59
3.8 Outcast dogs: life in animal shelters	62
3.9 Conclusions for the future	65
Further reading	65
4 A comparative approach to <i>Canis</i>	67
4.1 Introduction	67
4.2 Putting things into perspective: an overview of <i>Canis</i>	67
4.2.1 Systematic relationships and geographic distribution	67
4.2.2 The evolution of <i>Canis</i>	68
4.2.3 The ecology and dynamics of group living in some canids	71
4.3 An overview of wolves	74
4.3.1 Geographic distribution and systematic relationships	75
4.3.2 Evolution of the wolf	76
4.3.3 Behavioural ecological aspects	79
4.3.4 Social relationships between and within wolf packs	81
4.3.5 A comparison: social organization in free-ranging dogs	86
4.4 Wolf and dog: similarities and differences	89
4.4.1 Morphological traits	90
4.4.2 Behavioural comparisons	90
4.5 Conclusions for the future	92
Further reading	93
5 Domestication	95
5.1 Introduction	95
5.2 Human perspective on dog domestication	95
5.3 Archaeology faces phylogenetics	101
5.3.1 The archaeologists' story: looking at archaeological evidence	101
5.3.2 The geneticists' story: evolutionary genetic evidence	109

5.4	Some concepts of evolutionary population biology	117
5.4.1	The question of founder population(s)	117
5.4.2	On the nature of selection	118
5.4.3	Changes in reproductive strategy and effects on generation times	119
5.5	Emergence of phenotypic novelty	119
5.5.1	Mutation	120
5.5.2	Hybridization	123
5.5.3	Directional trait selection	124
5.5.4	Selection for plastic phenotypes	125
5.5.5	Heterochrony	126
5.5.6	The 'mysterious laws' of correlation	129
5.6	A case study of domestication: the fox experiment	131
5.6.1	The founding foxes and behavioural selection	131
5.6.2	Changes in early development	133
5.6.3	Changes in the reproductive cycle	134
5.6.4	Have we got domesticated foxes?	135
5.7	Conclusions for the future	136
	Further reading	136
6	The perceptual world of the dog	137
6.1	Introduction	137
6.2	Comparative perspectives	137
6.2.1	Cognitive aspects of perception	138
6.2.2	Experimental approach to study perceptual abilities	139
6.3	Vision	139
6.3.1	Physical processing	139
6.3.2	Neural processing and visual ability	141
6.3.3	Perception of complex visual images	142
6.4	Hearing	142
6.4.1	Physical processing	142
6.4.2	Neural processing and hearing ability	142
6.4.3	Perception of complex sound forms	143
6.5	Olfaction	144
6.5.1	Physical processing	144
6.5.2	Neural processing and olfactory ability	144
6.5.3	Categorization and matching in working situation	147
6.5.4	Perception of natural substances and conspecific odours	149
6.6	Conclusions for the future	150
	Further reading	150
7	Physical-ecological cognition	151
7.1	Introduction	151
7.2	Orientation in space	151
7.2.1	Path following	152
7.2.2	Beacons	152
7.2.3	Landmarks	152
7.2.4	Egocentric orientation	154

7.3 Spatial problem solving	155
7.4 Knowledge about objects	156
7.5 Memory for hidden objects	158
7.6 Folk physics in dogs?	160
7.6.1 Means–end connections	161
7.6.2 ‘Gravity’	162
7.7 Conclusions for the future	162
Further reading	163
8 Social cognition	165
8.1 Introduction	165
8.2 The affiliative aspects of social relationships	166
8.3 The agonistic aspects of social relationships	170
8.3.1 Classification of aggression in dogs	172
8.3.2 Is there an ethological description of aggressive behaviour in dogs?	172
8.3.3 Decreased aggression in dogs?	173
8.3.4 Organization of aggressive behaviour and the role of learning	173
8.3.5 Reaction to human agonistic signals	174
8.4 Communication in a mixed-species group	177
8.4.1 Visual communication	178
8.4.2 Acoustic communication	185
8.5 Play	189
8.6 Social learning in dogs	191
8.7 Social influence	193
8.8 Cooperation	196
8.9 Social competence	197
8.10 Conclusions for the future	200
Further reading	200
9 Development of behaviour	201
9.1 Introduction	201
9.2 What are developmental ‘periods’?	201
9.3 Rethinking developmental periods in dogs	205
9.3.1 Neonatal period	206
9.3.2 Transition period	206
9.3.3 Socialization period	207
9.3.4 Juvenile period	208
9.4 Sensitive periods in development	209
9.5 Attraction and attachment	214
9.6 Early experience and its influence on behaviour	216
9.7 Prediction of behaviour: ‘Puppy testing’	217
9.8 Conclusions for the future	219
Further reading	219
10 Temperament and personality	221
10.1 Introduction	221

10.2 Descriptive approach to personality	223
10.2.1 'Knowing', observing, or testing	223
10.2.2 Describing behaviour: assessment and coding	224
10.2.3 The construction of personality	225
10.3 Functional approach to personality	226
10.4 Mechanistic approach	230
10.4.1 Insights from genetics	230
10.4.2 Physiological correlates of personality traits	231
10.5 Conclusions for the future	234
Further reading	235
11 Afterword: Heading towards 21st-century science	237
11.1 Comparare necesse est!	237
11.2 Natural model	237
11.3 Evolving dogs	237
11.4 Behavioural modelling	239
11.5 Ethical implications and researchers' mission	240
11.6 Dog genome and bioinformatics	241
11.7 'Paws in hands'	241
References	243
Index	267