## Contents

	Aggression more generally		
1	Introduction		1
1.1	Overview		1
1.2	A definition of groups		2
1.3	Book structure		4
52	ted parentai care		
2	The benefits of group formation		6
2.1	Introduction		80
2.1	y and concentrations to read upon the concentration of the		6
2.2	Anti-predator vigilance 2.2.1 The classical many-eyes theory		8
	<ul><li>2.2.1 The classical many-eyes theory</li><li>2.2.2 How individual vigilance works</li></ul>		8
			9
			10
	1 Broup rightmoo		12
22	2.2.5 Related issues Dilution of risk		12
2.3	2.3.1 Avoidance, dilution, and abatement	4.1.3	13
	2.3.2 Predator swamping		13
251	2.3.3 The Selfish herd		17 17
	2.3.4 Defence against parasites		17
2.4	Predator confusion		19
2.4	2.4.1 Theory		19
	2.4.2 Empirical support for theoretical predictions		20
	2.4.3 Cognitive limitations		20
	2.4.4 Communal defence against predators		22
	2.4.5 Predator learning		23
2.5	Foraging benefits to grouping		23
2.5	2.5.1 Benefits for predators		23
	2.5.2 Finding food		25
2.6	Finding a mate		32
2.7	Conserving heat and water		34
2.8	Reducing the energetic costs of movement		36
	2.8.1 Introduction		36
	2.8.2 Movement in water		37

	2.8.3 Movement in air	38
2.9	Summary and conclusions	40
3	Some costs to grouping	41
3.1	Introduction	41
3.2	Increased attack rate on larger groups	42
3.3	Foraging in a group	46
	3.3.1 Kleptoparasitism	47
	3.3.2 Aggression more generally	47
	3.3.3 Pseudo-interference	48
	3.3.4 Shadow interference of sit and wait predators	48
	3.3.5 Just getting in each other's way	49
	3.3.6 Prey response to detected predators	50
	3.3.7 A note on generality	51
3.4	Increased parasite burdens	51
3.5	Misdirected parental care	52
	3.5.1 Cuckoldry	52
	3.5.2 Brood parasitism and adoption	53
3.6	Summary and conclusions	54
4	The size of a group	55
	2.2.2 How individual vigilance works	
4.1	Introduction also bivibil neewind polyaget not another C.S.S.	55
	4.1.1 Combining costs and benefits of grouping	55
	4.1.2 An illustrative example	56
	4.1.3 The shape of the fitness function	56
4.2	Are optimal group sizes likely to be seen in nature?	58
	4.2.1 An argument why groups should be larger than optimal	58
	4.2.2 Refinements of the argument	60
	4.2.3 The role of relatedness	61
	4.2.4 The influence of competition	62
	4.2.5 The effect of dominance hierarchies	63
20	4.2.6 Empirical evidence for active recruitment to foraging groups	63
4.3	Observed group sizes in nature	68
	4.3.1 Social carnivores	68
	4.3.2 Data from other taxa	69
23	4.3.3 Distribution of group sizes	69
4.4	Summary and conclusions	71
5	Spatial heterogeneity of costs and benefits	
	within groups	73
	Reducing the energetic costs of movement	2.8
5.1	Introduction	73
5.2	Group structure and spatial positions: definitions	74
5.3		75

5.4.1       Energy intake       77         5.4.2       Energy expenditure       78         5.4.3       Net-energy payoff       79         5.5       Predation risk       80         5.5.1       Stationary groups       80         5.5.2       Mobile groups       80         5.6       Parasites       83         5.7       Reproductive success       83         5.8       Dominance status       84         5.9       Trade-offs between different fitness currencies       85         5.10       Summary and conclusions       86         6       Heterogeneity and homogeneity of group membership       87         6.1       Introduction       87         6.2       Theory of assortativeness       88         6.3       The influence of predation on assortment       89         6.3.1       Predator preference for odd prey (the oddity effect)       90         6.3.2       Evidence for the oddity effect from prey behaviour       93         6.3.4       Frequency-independent preferences       94         6.3.5       Reduced vigilance in mixed species groups       96         6.4.4       The role of species       97         6.4.2       The rol
5.4.3       Net-energy payoff       79         5.5       Predation risk       80         5.5.1       Stationary groups       80         5.5.2       Mobile groups       80         5.6       Parasites       83         5.7       Reproductive success       83         5.8       Dominance status       84         5.9       Trade-offs between different fitness currencies       85         5.10       Summary and conclusions       86         6       Heterogeneity and homogeneity of group membership       87         6.1       Introduction       87         6.2       Theory of assortativeness       88         6.3       The influence of predation on assortment       89         6.3.1       Predator preference for odd prey (the oddity effect)       90         6.3.2       Evidence for the oddity effect from prey behaviour       93         6.3.3       Predator preference for common prey       93         6.3.4       Frequency-independent preferences       94         6.3.5       Reduced vigilance in mixed species groups       96         6.4       Evidence for the evolution of group mate preferences in prey       97         6.4.1       The role of species       97<
5.5       Predation risk       80         5.5.1       Stationary groups       80         5.6       Parasites       83         5.7       Reproductive success       83         5.8       Dominance status       84         5.9       Trade-offs between different fitness currencies       85         5.10       Summary and conclusions       86         6       Heterogeneity and homogeneity of group membership       87         6.1       Introduction       87         6.2       Theory of assortativeness       88         6.3       The influence of predation on assortment       89         6.3.1       Predator preference for odd prey (the oddity effect)       90         6.3.2       Evidence for the oddity effect from prey behaviour       93         6.3.4       Frequency-independent preferences       94         6.3.5       Reduced vigilance in mixed species groups       96         6.4       Evidence for the evolution of group mate preferences in prey       97         6.4.1       The role of species       97         6.4.2       The role of parasitism       99         6.4.4       The role of familiarity       100
5.5.1       Stationary groups       80         5.5.2       Mobile groups       80         5.6       Parasites       83         5.7       Reproductive success       83         5.8       Dominance status       84         5.9       Trade-offs between different fitness currencies       85         5.10       Summary and conclusions       86         6       Heterogeneity and homogeneity of group membership       87         6.1       Introduction       87         6.2       Theory of assortativeness       88         6.3       The influence of predation on assortment       89         6.3.1       Predator preference for odd prey (the oddity effect)       90         6.3.2       Evidence for the oddity effect from prey behaviour       93         6.3.4       Frequency-independent preferences       94         6.3.5       Reduced vigilance in mixed species groups       96         6.3.6       Differential anti-predatory abilities within a group       96         6.4       Evidence for the evolution of group mate preferences in prey       97         6.4.1       The role of species       97         6.4.2       The role of body length and colour       98         6.4.3       <
5.5.2       Mobile groups       80         5.6       Parasites       83         5.7       Reproductive success       83         5.8       Dominance status       84         5.9       Trade-offs between different fitness currencies       85         5.10       Summary and conclusions       86         6       Heterogeneity and homogeneity of group membership       87         6.1       Introduction       87         6.2       Theory of assortativeness       88         6.3       The influence of predation on assortment       89         6.3.1       Predator preference for odd prey (the oddity effect)       90         6.3.2       Evidence for the oddity effect from prey behaviour       93         6.3.3       Predator preference for common prey       93         6.3.4       Frequency-independent preferences       94         6.3.5       Reduced vigilance in mixed species groups       96         6.4       Evidence for the evolution of group mate preferences in prey       97         6.4.1       The role of body length and colour       98         6.4.3       The role of familiarity       100
5.5.2       Mobile groups       80         5.6       Parasites       83         5.7       Reproductive success       83         5.8       Dominance status       84         5.9       Trade-offs between different fitness currencies       85         5.10       Summary and conclusions       86         6       Heterogeneity and homogeneity of group membership       87         6.1       Introduction       87         6.2       Theory of assortativeness       88         6.3       The influence of predation on assortment       89         6.3.1       Predator preference for odd prey (the oddity effect)       90         6.3.2       Evidence for the oddity effect from prey behaviour       93         6.3.3       Predator preference for common prey       93         6.3.4       Frequency-independent preferences       94         6.3.5       Reduced vigilance in mixed species groups       96         6.3.6       Differential anti-predatory abilities within a group       96         6.4       Evidence for the evolution of group mate preferences in prey       97         6.4.2       The role of body length and colour       98         6.4.3       The role of familiarity       100
5.6Parasites835.7Reproductive success835.8Dominance status845.9Trade-offs between different fitness currencies855.10Summary and conclusions866Heterogeneity and homogeneity of group membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of familiarity100
5.7Reproductive success835.8Dominance status845.9Trade-offs between different fitness currencies855.10Summary and conclusions866Heterogeneity and homogeneity of group membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
5.8Dominance status845.9Trade-offs between different fitness currencies855.10Summary and conclusions866Heterogeneity and homogeneity of group membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
5.9Trade-offs between different fitness currencies855.10Summary and conclusions866Heterogeneity and homogeneity of group membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
5.10Summary and conclusions866Heterogeneity and homogeneity of group membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
membership876.1Introduction876.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
6.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of parasitism996.4.4The role of familiarity100
6.2Theory of assortativeness886.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of parasitism996.4.4The role of familiarity100
6.3The influence of predation on assortment896.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.3The role of parasitism996.4.4The role of familiarity100
6.3.1Predator preference for odd prey (the oddity effect)906.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of familiarity100
6.3.2Evidence for the oddity effect from prey behaviour936.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.3.3Predator preference for common prey936.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.3.4Frequency-independent preferences946.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.3.5Reduced vigilance in mixed species groups966.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.3.6Differential anti-predatory abilities within a group966.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.4Evidence for the evolution of group mate preferences in prey976.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.4.1The role of species976.4.2The role of body length and colour986.4.3The role of parasitism996.4.4The role of familiarity100
6.4.3 The role of parasitism996.4.4 The role of familiarity100
6.4.3 The role of parasitism996.4.4 The role of familiarity100
6.4.4 The role of familiarity 100
6.4.5 The role of kinship 100
6.5 Multi-species foraging groups 101
6.6 Consequences of inter-individual differences for optimal
group size 102
6.7Summary and conclusions102
7 Evolutionary considerations 104
7.1 Introduction 104
7.2 Individual differences: artificial selection 104
7.3 Population differences 106
7.3.1 Testing for population differences 106
7.4 Species differences 110
7.4.1 Pathways towards the evolution of groups 113
7.5 Groups as units of selection 119
7.6 Summary and conclusions 121

8	Environmental effects on grouping behaviour	123
8.1	Introduction	123
8.2	Ontogenetic constraints on grouping: fish shoaling behaviour	123
8.3	Ontogenetic shift in sociality: the spiny lobster	125
8.4	The role of rearing conditions: caste determination and	120
0.1	division of labour in the honey bee	126
8.5	Behavioural changes induced by crowding: the desert locust	120
8.6	The role of learning	130
8.7	Parasite-mediated changes in behaviour	132
8.8	Summary and conclusions	135
9	Mechanisms	137
9.1	Introduction	137
9.2	Recognition of suitable group mates	137
9.3	Inter-individual distance regulation: attraction and repulsion	138
9.4	Group formation	140
9.5	Collective behaviour	140
10	9.5.1 Locomotion	140
	9.5.2 Positioning behaviour and leadership	142
	9.5.3 Group structure	143
	9.5.4 Collective foraging	145
	9.5.5 Teams	146
9.6	Assessment of group size and group composition	146
9.7	Group size distributions	140
9.8	Summary and conclusions	150
10	Conclusions	
10		151
10.1	Introduction	151
10.2	Group size	151
	10.2.1 Individual-based models of group size	152
	10.2.2 Population density and group size	153
10.3	Comparative studies	155
10.4	Evolution of grouping	156
10.5	Group composition	156
10.6	Signalling	157
10.7	Short-term behavioural change	157
10.8	Concluding remarks	158
Ref	erences	159
Aut	hor Index	189
Gar	neral Index	100
Ger	ierai illuez	199