

Contents

<i>Preface</i>	xiii
1 Introduction	1
1.1 Introduction	2
1.2 The two species in taxonomic and biogeographic context	7
1.2.1 Penguins	8
1.2.2 Skuas	10
1.3 Research philosophy and definitions	16
1.3.1 Research philosophy	16
1.3.2 Definitions	18
2 The study area: Ross Island and the Cape Bird penguin colonies	20
2.1 Introduction	20
2.2 The Cape Bird penguin colonies	22
2.3 The Northern Colony	24
2.3.1 The penguin breeding groups	27
2.3.2 Skua territories	28
2.4 The Cape Bird environment	30
2.4.1 The local climate	31
2.4.2 Impact of environmental factors on the birds	34
2.5 General methods	37
2.5.1 For research on penguins	37
2.5.2 For research on skuas	39
2.5.3 Observation	40
2.5.4 Breeding cycles and key stages	42
2.6 The study areas within the colony	45
3 The range of foods available to the skuas at Cape Bird during the breeding season	48
3.1 Introduction	48
3.2 The foraging range of penguins and skuas at Cape Bird	48
3.3 Foods available within the foraging range	53
3.3.1 Zooplankton	54
3.3.2 Fish and squid as skua food	55

viii	<i>Contents</i>	
	3.3.3 Food available to skuas from seals	58
	3.3.4 Food gained by predation and scavenging on birds	62
	4 The biomass of penguin eggs and chicks on the Northern Colony	68
4.1	Introduction	68
4.2	Estimating numbers and biomass for the penguin colony	68
	4.2.1 Numbers of penguin nests on the colony each year	69
	4.2.2 Estimating the total numbers of eggs and chicks on the Northern Colony throughout the breeding season	72
	4.2.3 Estimating egg and chick biomass on the colony	73
4.3	The estimates of egg and chick numbers and the total biomass on the Northern Colony throughout each season	74
	5 Factors of penguin breeding biology that constrain or assist skua predation of eggs and chicks	80
5.1	Introduction	80
5.2	Constraints imposed on the skuas by the tight synchrony of the penguin breeding cycle and the relative timing of the cycles of the two species	81
5.3	Constraints imposed on the movements of skuas in the colonies and on the selection of prey nests because of the colonial nesting habit of penguins	82
	5.3.1 Limitations on skua access to nests because of neighbours	82
	5.3.2 Protection by being alerted to skuas in the area by neighbours	83
	5.3.3 Protection of the eggs and chicks in the nest	85
	5.3.4 Numbers of adults within the breeding group	89
5.4	Constraints imposed on skuas as predators through the size and strength of the prey	97
	5.4.1 Differences in the size of adult penguins and skuas	97
	5.4.2 Constraints imposed on prey availability through the growth and increasing maturity of the penguin chicks	98
5.5	Aspects of penguin behaviour and biology apparently facilitating skua predation	101
	5.5.1 Penguin breeding behaviour	101
	5.5.2 Rejection of eggs and chicks outside the nest	101
	5.5.3 Orientation of incubating and guarding penguins in relation to wind direction	101
	5.5.4 Breakdown of group structure at the beginning of the post-guard stage	103
	5.5.5 Chicks outside the breeding group area	106
5.6	Constraints on skua activity because of the need to protect their own eggs and chicks	108
	6 Description of scavenging and predatory behaviour of skuas and the defensive behaviour of penguins	110
6.1	Introduction	110
6.2	Searching behaviour: hunting flights and observation of the penguins	111
6.3	Scavenging	114
	6.3.1 Scavenging outside the margin of the breeding group	114

<i>Contents</i>	ix
6.3.2 Scavenging among nesting penguins	114
6.3.3 Mixed scavenging and attack behaviour	116
6.4 Predation on eggs and chicks at defended nests	117
6.4.1 Opportunistic attacks	117
6.4.2 Sustained attacks	121
6.5 Attacks on unguarded chicks: the post-guard stage	128
6.5.1 Phase one: separating the target from other chicks and adults	131
6.5.2 Phase two: subduing and killing large chicks	133
6.6 Comparison between skua agonistic and predatory behaviour	136
6.7 The behaviour of penguins in defence against skuas	139
6.7.1 Protection afforded to individual nests by the colony structure	141
6.7.2 Nest defence zones	142
6.7.3 Penguin defensive responses to skua activity on the ground near the nest	144
6.7.4 Penguin defensive responses to skuas in flight above the breeding group	149
6.7.5 Aggressive defence by adult penguins of chicks outside the breeding group	149
6.7.6 Defensive behaviour by chicks attacked outside the breeding group	151
7 The diversity and intensity of skua foraging behaviour on the penguin colony	155
7.1 Introduction	155
7.2 The study areas within the Northern Colony	155
7.3 Observing, recording and analysing skua foraging behaviour	157
7.3.1 The development of the coded ethogram used to record observations of foraging	157
7.3.2 The observation logs and the way the recording was carried out	161
7.3.3 Sampling and recording behaviour	162
7.3.4 The analysis of the coded behaviour data	163
7.3.5 Taking the skua behaviour at different stages of the penguin breeding cycle into account in the analyses	163
7.4 The proportion of time spent by the skuas in interactions with the penguins	164
7.4.1 Changes in foraging activity on the penguin colony during the season	166
7.4.2 Differences among seasons in skua interest and activity	166
7.4.3 Comparisons between the two study areas	167
7.4.4 Were the pairs equally interested in the penguins?	168
7.4.5 Were the two birds of the pair equally interested in the penguins?	170
7.5 The proportion of time away from the territory	170
7.6 The behaviour of skuas interacting with penguins – the behaviour of predation and scavenging	173
7.6.1 The frequency of the different attack forms	174
7.6.2 Individual differences among the skuas	177
7.6.3 Overall differences in searching, scavenging and predation	178

x	<i>Contents</i>	
7.7	Foraging sequences during the day and season	185
7.7.1	The sequences of behaviour during a foraging bout	185
7.7.2	The attacks of a strong predator: a sequence of attacks by the male of pair 25 on H Block	187
7.7.3	The pattern of activity across days	195
7.8	The relative success of the different forms of attack on penguins	203
8	The amount of food taken by the skuas from the penguin colony	211
8.1	Introduction	211
8.2	The numbers of eggs and chicks taken by the skuas	214
8.2.1	Numbers of prey items taken at different stages of the penguin breeding cycle	214
8.2.2	Comparison of H and EF skuas	215
8.2.3	A check on the observation and prey remains statistics: the average numbers of eggs and chicks lost each year from the breeding groups on H and EF blocks	217
8.3	The amount of food taken by the skuas on the penguin colony and its energy content	219
8.3.1	Mass and energy content of penguin eggs and chicks	220
8.3.2	Food taken by individual pairs during the different penguin life-cycle stages	236
8.3.3	Average intake levels for all pairs in the local area	238
9	The costs and returns of foraging at the colony and at sea	240
9.1	Introduction	240
9.2	Foraging at sea	242
9.2.1	Obtaining records of foraging skuas	242
9.2.2	The energy returns from fishing	243
9.2.3	Energy costs of foraging at sea	245
9.3.	The energy costs and gains from foraging on the penguin colony	258
9.3.1	Simplifying the variables	258
9.3.2	The energy costs of foraging on the penguin colony	260
9.4	The energy equation of foraging at sea versus foraging on the penguin colony	266
9.5	Why don't all the skuas with penguins exploit them strongly?	269
9.6	Assessing the food sufficiency of pairs foraging on the penguin colony	274
9.6.1	Daily energy requirements	275
9.6.2	Comparing the field metabolic rate with the estimated amounts gained each day from the penguin colony	277
10	Immediate impact of the skuas on penguin breeding	281
10.1	Introduction	281
10.1.1.	Are skuas predators?	283
10.2	Methods used in measuring skua impact on breeding penguins	283
10.3	Place of breeding as a factor in the breeding success of penguins	287
10.3.1	Location of breeding group within the penguin colony	287
10.3.2	Nest location <i>within</i> the breeding group	291

<i>Contents</i>	xi
10.4 The role of disturbance in skua predation and scavenging	297
10.4.1 Amount and form of disturbance to breeding penguins	297
10.4.2 The possible role of disturbance in production of carrion on the colony	302
10.4.3 Possible role of disturbance on the timing of the onset of the post-guard stage	304
10.5 Selection of prey on the penguin colony	308
10.5.1 Records of prey taken and prey selection	309
10.5.2 Carrion present on the colony: deserted and displaced eggs, displaced and dead chicks	312
10.5.3 Selection of live chicks	318
10.6 Skuas: predator or scavenger – the exclosure experiments	322
10.6.1 The design and analysis of the exclosure experiments	323
10.6.2 Results of the exclosure experiments to measure breeding success in the absence of skua activity	328
10.7 Predator or scavenger: conclusions on the effectiveness of predation: evidence from comparing penguin breeding success in areas with high and low predator to prey ratios	333
11 Appreciating the penguins: is it worth living with the penguins and do skuas appreciate the advantage?	337
11.1 Introduction	337
11.2 The breeding success of skuas in different locations within and near the penguin colony	338
11.2.1 Breeding success over five seasons of skuas at the penguin colony	343
11.2.2 Breeding success of skuas in different geographic areas at Cape Bird	347
11.3 Date of egg-laying	360
11.4 Do skuas appear to appreciate the advantage of nesting close to the penguin colony	363
11.4.1 Taking up territories at the beginning of the breeding season	363
11.4.2 Evidence for attraction to the penguins later within the season in changes to territories	368
11.4.3 Changes across seasons: the longer term changes	369
11.4.4 The club of non-breeding skuas	372
11.5 Conclusions on the evidence of attractiveness	374
12 Associating together: the longer-term implications	376
12.1 Introduction	376
12.2 Breeding site selection and disposition of penguins and skuas within the breeding areas	377
12.3 The breeding seasons: dependent synchrony or fortuitous coincidence?	381
12.3.1 Relationship between the breeding seasons of the two species: seasonal timing and breeding season synchrony	381
12.3.2 The Cape Bird summer: the duration of suitable breeding conditions	382

xii	<i>Contents</i>	
	12.3.3 The minimum time needed for breeding	388
	12.3.4 The timing of the breeding cycles at Cape Bird within the habitable period	393
	12.4 Degree of synchronicity of breeding seasons	396
	12.5 Timing of the cycles in relation to universal proximate factors	396
	12.6 Conclusions on association	399
	13 Synthesis	401
	Appendices	413
	Appendix 1	413
	Appendix 2	420
	Appendix 3	423
	Appendix 4	429
	Appendix 5	431
	<i>References</i>	433
	<i>Index</i>	444