

# Contents

*List of figures* viii

*List of tables* x

*Preface* xiv

<b>1</b>	<b>The Arctic Skuas of Fair Isle</b>	1
	1.1 The Arctic Skua and its breeding grounds	1
	1.2 Catching the Arctic Skuas	10
	1.3 Studying the birds and recording their data	14
	1.4 Classifying the phenotypes	19
	1.5 Ecology and genetics of Arctic Skuas	23
	1.6 Relationships with other species of Skuas	28
<b>2</b>	<b>Numbers and distribution</b>	32
	2.1 Surveys of breeding colonies	32
	2.2 Changes in population numbers and status	37
	2.3 Regulation of numbers by predation, competition and food	43
	2.4 Migration	47
	2.5 Distribution of phenotypes: clines in frequencies	50
<b>3</b>	<b>Feeding behaviour and ecology</b>	60
	3.1 Kleptoparasitism by Arctic Skuas in the breeding season and on migration	60
	3.2 Selection of Arctic Skuas as a result of kleptoparasit- ism	67
	3.3 Energetics of feeding behaviour	69
	3.4 Territories as feeding areas	72
<b>4</b>	<b>Breeding ecology</b>	81
	4.1 The breeding season	81
	4.2 Egg laying and incubation	84
	4.2.1 Clutch size	85
	4.2.2 Incubation period, order of laying the eggs and breeding experience	85
	4.2.3 Incubation period and phenotype	88

vi	<i>Contents</i>	
	4.3 Fledging the chicks	91
	4.3.1 Fledging period and phenotype	98
<b>5</b>	<b>Genetics</b>	100
	5.1 Genetic analysis of matings between phenotypes	100
	5.1.1 Chicks produced by matings	100
	5.1.2 Chicks recaptured as breeding adults	106
	5.2 Frequencies of phenotypes in the Fair Isle population	108
	5.3 Heritability of breeding dates	110
	5.4 Heritability of clutch size and fledging success	116
<b>6</b>	<b>Demography and selection</b>	120
	6.1 Survival rates of the phenotypes	123
	6.1.1 Effects of shooting on survival in the Fair Isle population	127
	6.2 Age at maturity and reproductive rate in relation to age	132
	6.3 Intrinsic rates of increase and components of selection	139
<b>7</b>	<b>Sexual behaviour</b>	145
	7.1 Territoriality, pair formation and mating behaviour	145
	7.1.1 Agonistic behaviour in defence of territory	145
	7.1.2 Pair formation and mate selection	151
	7.1.3 Mating behaviour and nest building	155
	7.2 Measuring territory size	159
	7.3 Territory size, phenotype and breeding time	164
	7.4 Sexual selection and the evolution of territoriality	172
<b>8</b>	<b>Sexual selection</b>	180
	8.1 Darwin's theory of sexual selection	180
	8.2 Sexual selection and the evolution of mating preferences	184
	8.3 Sexual selection in polygynous and monogamous birds	189
	8.4 Sexual selection in the Arctic Skua	193
	8.4.1 Males pairing with a new female	194
	8.4.2 Comparison of males in new and second-year pairs	197
	8.4.3 Male experience and pairing	200
	8.4.4 Breeding dates of males and females	201
	8.5 Sexual selective values of Arctic Skua phenotypes	203
<b>9</b>	<b>Genetic models of sexual selection in birds</b>	210
	9.1 Female preferences and male competition in monogamous birds	210
	9.2 Genetic models of preferential mating	215

<i>Contents</i>	vii
9.2.1 Preferences for two phenotypes with dominance	216
9.2.2 Separate preferences for each of the genotypes	222
9.2.3 Preference for a dominant phenotype with natural selection against it	225
9.3 Genetic models of male competition	232
9.3.1 Competition between dominant and recessive phenotypes	233
9.3.2 Competition between each genotype	234
9.3.3 Natural selection with competition between dominant and recessive phenotypes	236
9.4 Preferential mating with assortment	238
<b>10 Mating preferences of the Arctic Skua</b>	<b>244</b>
10.1 Models of preferential mating	244
10.2 Estimation of mating preferences	247
10.3 Assortative mating	255
10.4 Summary of evidence for female choice	259
10.5 The mechanism of sexual selection: conclusion	262
<b>11 Conclusions</b>	<b>264</b>
<b>Appendix A Rates of increase of bird populations</b>	<b>271</b>
A.1 Estimation of exponential rates of increase	271
A.2 Estimation of survival and reproductive rates	274
A.3 Rates of increase of Arctic Skuas on Fair Isle and Foula	276
<b>Appendix B Analysis of variance of a <math>2 \times r</math> table with unequal numbers of observations</b>	<b>285</b>
<b>Appendix C Statistical analysis of assortative and disassortative mating in polymorphic birds</b>	<b>291</b>
C.1 Introduction to the theory of assortative mating	291
C.2 Models of assortative and disassortative mating	293
C.3 Analysis of data	297
C.3.1 Analysis of $\chi^2$ of data of mating frequencies	301
C.4 Assortative and disassortative mating of melanistic birds	304
C.4.1 Assortative mating of the Arctic Skua	304
C.4.2 Disassortative mating of the feral pigeon and Eleonora's Falcon	306
<i>References</i>	309
<i>Index</i>	315