

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

The Arctic Skua

*a study of the ecology and evolution
of a seabird*

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

The Arctic Skua

*a study of the ecology and
evolution of a seabird*

PETER O'DONALD, Sc.D

Fellow and Tutor, Emmanuel College, Cambridge

ILLUSTRATED BY ROBERT GILLMOR

CAMBRIDGE UNIVERSITY PRESS

CAMBRIDGE

LONDON NEW YORK NEW ROCHELLE

MELBOURNE SYDNEY

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

CAMBRIDGE UNIVERSITY PRESS

Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo, Delhi

Cambridge University Press

The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org

Information on this title: www.cambridge.org/9780521113342

© Cambridge University Press 1983

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 1983

This digitally printed version 2009

A catalogue record for this publication is available from the British Library

Library of Congress Catalogue Card Number: 82-12782

ISBN 978-0-521-23581-5 hardback

ISBN 978-0-521-11334-2 paperback

Contents

List of figures viii

List of tables x

Preface xiv

1	The Arctic Skuas of Fair Isle	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
2	Numbers and distribution	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
3	Feeding behaviour and ecology	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
4	Breeding ecology	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
5	Genetics	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
6	Demography and selection	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
7	Sexual behaviour	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
8	Sexual selection	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
9	Genetic models of sexual selection in birds	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
10 Mating preferences of the Arctic Skua	244
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
11 Conclusions	264
Appendix A Rates of increase of bird populations	271
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
Appendix B Analysis of variance of a $2 \times r$ table with unequal numbers of observations	285
Appendix C Statistical analysis of assortative and disassortative mating in polymorphic birds	291
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 χ^2 of data of mating frequencies	301
C.4 Assortative and disassortative mating of melanic 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

List of figures

1.1 Map of Fair Isle showing the limits of the Arctic Skua colony in different years	3
1.2 An Arctic Skua's nest with eggs	5
1.3 A funnel trap for catching Arctic Skuas	13
1.4 A pale chick; its belly feathers shown in close up	22
1.5 An intermediate chick; its belly feathers shown in close-up	24
1.6 A dark chick; its belly feathers shown in close-up	25
1.7 Evolutionary tree of the Stercorariidae	30
2.1 Map of Foula	35
2.2 Map of Shetland, Orkney and Scotland showing the positions of the main Arctic Skua colonies	36
2.3 Map of the Northern Hemisphere showing the rough limits of the Arctic Skua's range	38
2.4 Rates of increase of pairs of Arctic Skuas on Fair Isle	42
2.5 Map showing places where Arctic Skuas ringed on Fair Isle have been recovered	49
2.6 Map of the Northern Hemisphere showing roughly where melanistic Arctic Skuas occur at frequencies of 75, 50 and 25 per cent	51
2.7 Plot of the frequencies of melanics along the cline showing the S-shaped curve fitted to the cline	53
3.1 Percentage of successful attacks on terns when Arctic Skuas attack in ones, twos, threes, fours or fives	62
3.2 Maps of Northern Norway where Andersson and Götmark studied the feeding behaviour of pairs of Arctic Skuas	75
4.1 The breeding cycle of the Arctic Skua on Fair Isle	84
5.1 Breeding dates of parents and offspring showing regression of offspring value on parental value	114
7.1 The 'Jump' in counter-attack to the 'Swoop'	148
7.2 Aggressive and intimidated upright postures	151
7.3 The 'Begging' and 'Squeaking' attitudes	157
7.4 Willing attitude of female and copulation	158
7.5 Map of polygonal territories on Wirvie Brecks and Brae of Restensgeo in 1977	163

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

<i>List of figures</i>	ix
7.6 Map of polygonal territories on Wirvie Brecks and Brae of Restensgeo in 1978	164
7.7 Relationship of territory size to breeding date (males)	169
8.1 Distributions of breeding dates of new and second-year pairs	199
10.1 Theoretical distributions of the breeding dates of the phenotypes	255

Figures 7.1, 7.2, 7.3 and 7.4 were drawn by Robert Gillmor on the basis of photographs and drawings in a paper by Perdeck (1963)

List of tables

1.1 Comparative measurements of Skuas	29
2.1 Estimates of pairs of Arctic Skuas on Foula, Shetland	39
2.2 Estimates of pairs of Arctic Skuas on Noss, Shetland	40
2.3 Estimates of pairs of Arctic Skuas on Hermaness, Unst, Shetland	41
2.4 Numbers of pairs of Arctic Skuas on Fair Isle, Shetland	41
2.5 Dates when the first Bonxies and Arctic Skuas return to Fair Isle and lay their eggs	44
2.6 Predation of Arctic Skuas by Bonxies on Foula, Shetland	45
2.7 Numbers of phenotypes counted at different points along the cline	52
2.8 Analysis of χ^2 of Southern's data of the cline	54
2.9 Phenotypic frequencies in Iceland	54
2.10 Phenotypic frequencies in Shetland	55
3.1 Numbers of attacks on terns and Puffins by one or more Arctic Skuas	62
3.2 Means and standard errors of the times in seconds of attacks by Arctic Skuas	63
3.3 Outcome of chases at different distances from the cliff and heights above ground	65
3.4 Analysis of χ^2 of chases at different distances and in different directions from the cliff	66
3.5 Time spent chasing Puffins when different percentages of chases are successful	71
3.6 Prey items in Arctic Skua droppings at Varanger in 1977 and 1978	77
3.7 Prey items in Arctic Skua pellets	78
4.1 Hatching dates of established pairs from 1974–79	83
4.2 Clutch size of Arctic Skuas in relation to breeding date	86
4.3 The incubation period of the Arctic Skua	87
4.4 Incubation periods of first and second eggs	87
4.5 Incubation periods of new and old pairs	89
4.6 Incubation periods of the phenotypes	90
4.7 The fledging period of the Arctic Skua	92
4.8 Regression analysis of fledging period and breeding date	94

<i>List of figures</i>	xi
4.9 Fledging periods of new and old pairs in different years	95
4.10 Fledging periods of first and second chicks in different years	96
4.11 Fledging periods of phenotypes in different years	98
5.1 Chicks produced by matings in period 1951–58	101
5.2 Expected frequencies of pale, intermediate and dark progeny of each of the mating types	103
5.3 Chicks produced by different matings in the period 1973–79	105
5.4 Chicks recaptured as adults produced by parents of known phenotype	106
5.5 Adult phenotypes of offspring produced by different matings when dark-intermediates are classed with intermediates	107
5.6 Adult phenotypes of offspring produced by different matings when dark-intermediates are classed with darks	108
5.7 Breeding dates of parents and offspring	113
5.8 Clutch size of parents and offspring	116
5.9 Fledging success of parents and offspring	118
6.1 Survival of phenotypes from one breeding season to the next in the period 1948–62	128
6.2 Survival of phenotypes from one breeding season to the next in the period 1973–78	128
6.3 Mortality and survival of the phenotypes in different periods	131
6.4 Distributions of age at maturity of the phenotypes	132
6.5 Analysis of χ^2 of data on ages at maturity	136
6.6 Reproductive rates of ringed birds in their first and subsequent years of breeding	137
6.7 Reproductive rates of male and female phenotypes	138
6.8 Variations between phenotypes in reproductive rate and age at maturity	140
6.9 Intrinsic rates of increase and selective coefficients	141
6.10 Selection within each sex	143
7.1 Change of position of territory after change of mate	153
7.2 Fidelity of new and established pairs	156
7.3 Territory sizes of new and experienced males in new pairs	167
7.4 Territory sizes of males in periods 1974–75 and 1977–78	168
7.5 Test of homogeneity of regressions in different classes of males	170
7.6 Test of homogeneity of correlation coefficients in different classes of males	170
7.7 Breeding date and fledging success of the Arctic Skua	176
7.8 Example of probabilities of mating and resultant fitnesses when probability of mating is proportional to territory size	177
8.1 Breeding dates of melanic and non-melanic male Arctic Skuas in new pairs	195
8.2 Breeding dates of males in new pairs in periods 1948–62 and 1973–79	196
8.3 Breeding dates of males in new and second-year pairs	197
8.4 Breeding dates of new and experienced males in new pairs	201
8.5 Breeding dates of males and females in new pairs	202

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)xii *List of tables*

8.6	Fitness of pairs in relation to breeding date and years of breeding as a pair	204
8.7	Relationship of fledging success to breeding date in the Arctic Skua	206
9.1	Frequencies of preferential and random matings and the fertilities of matings as determined by preferences for both dominant and recessive phenotypes	218
9.2	Equilibrium frequencies and rates of approach to equilibrium in models with dominance and either polygynous or monogamous mating	222
9.3	Fertilities of matings with separate preferences for each genotype	224
9.4	Equilibrium frequencies and rates of approach to equilibrium in models with separate preferences for each genotype and either polygynous or monogamous mating	224
9.5	Frequencies of preferential and random matings and the fertilities of matings as determined by preferences for both dominant and recessive phenotypes	226
9.6	Fertilities of the matings with preferences for both dominant and recessive phenotypes	230
9.7	Frequencies of early and late matings and fertilities of matings determined by competition between dominant and recessive male phenotypes	234
9.8	Frequencies of early and late matings and fertilities of matings determined by competition between male genotypes	235
9.9	Fertilities of matings with natural selection and competition between dominant and recessive phenotypes	237
9.10	Fertilities of matings in a model of monogamous assortative mating	241
10.1	Breeding dates of melanic and non-melanic male Arctic Skuas in new pairs	246
10.2	Maximum likelihood (M.L.) estimates of female preferences when the models of preferential mating are fitted to the data of table 10.1	249
10.3	Data for analysis of χ^2	253
10.4	Analysis of χ^2 when Model 3P is fitted to the data of table 10.3	254
10.5	Matings between phenotypes of Arctic Skuas on Fair Isle 1973–79	256
10.6	Assortative mating of melanic and pale phenotypes of Arctic Skuas	258
A1	Expressions for the calculation of the values of R_0 , R_1 and R_2	279
A2	Total numbers of chicks fledged to individual birds breeding in successive years in the colony	280
A3	Breeding dates and chicks fledged in period 1948–62	281
B1	Means, numbers of values and expectations in a $2 \times r$ table	286
B2	Analysis of variance of a $2 \times r$ table with unequal numbers of observations	290

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

<i>List of tables</i>	xiii
C1 Frequencies of matings with and without assortment of phenotypes	294
C2 Probabilities of matings and correlations between mates in models of assortative and disassortative mating	296
C3 Estimates of parameters and values of information matrix	299
C4 Analysis of χ^2 for data of assortative or disassortative mating	303
C5 Analysis of assortative mating of melanic and pale phenotypes of the Arctic Skua	305
C6 Disassortative matings of each phenotype in a population of feral pigeons	307
C7 Disassortative mating of Eleonora's Falcon	308

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

Preface

This book describes the results of research spanning a period of 30 years. The late Kenneth Williamson began studying the Arctic Skuas of Fair Isle in 1948. Only 15 pairs were then nesting on the island. In 1957, Peter Davis took up the study, having succeeded Williamson as Warden of the Fair Isle Bird Observatory. As part of research for the Ph.D. degree of the University of Cambridge, I spent three years from 1958 to 1961 studying the genetics of the Arctic Skua. I was supported by a Nature Conservancy Research Studentship. This initial period of research on the Arctic Skuas ended in 1962 when Peter Davis left Fair Isle. By this time, 71 pairs were nesting on the island.

In 1970, R. J. Berry and Peter Davis published a paper analysing the breeding dates of the different phenotypes of the Arctic Skuas (Berry & Davis, 1970). They found that pale males, breeding for the first time, bred several days later on average than first-time, intermediate and dark males. They interpreted this as a behavioural adaptation of pale birds to their more northerly distribution where later breeding might be advantageous. At that time, I was working on models of Darwin's theory of sexual selection. The later breeding of certain male phenotypes in new pairs is exactly what the models predict, whereas the adaptation postulated by Berry and Davis should have been shown by all birds. This was obviously an opportunity to test Darwin's theory in a natural population. I successfully applied for a Research Grant from the Natural Environment Research Council (NERC) for the support of three years research, 1973–75. I later obtained another grant from NERC for the three years, 1976–79. In the period 1973–75, the grant allowed for the appointment of John F. Davis as a full-time research assistant. This second period of research on the Arctic Skuas of Fair Isle ended in 1979.

When John Davis and I began the second period of research in 1973, 106 pairs of Arctic Skuas were nesting on Fair Isle. John Davis devised the method of catching the adult breeding birds in funnel traps. This was much

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)*Preface*

xv

quicker than the clap nets previously used. Most of the breeding birds were caught and ringed in 1973. I am very pleased to acknowledge the great enthusiasm and energy which John Davis put into studying the Arctic Skuas. In 1975, Shoshana Ashkenazi assisted in our survey of the Arctic Skuas of Foula. Roger Broad, the new Warden of the Bird Observatory, gave much of his time to the skua study, particularly in helping to catch the birds. I am grateful for his very considerable help in 1976 after the first NERC grant had expired. Later, in 1978 and 1979, I was assisted by Jane French, a research student on an NERC Studentship, and Iain Robertson, who had succeeded Roger Broad as Warden of Fair Isle.

This book is a largely original account of the research on breeding behaviour, ecology and evolutionary genetics of the Arctic Skua. I have added a chapter on feeding behaviour (chapter 3) based on the published work of others, though with my own analyses of the data. Section 7.1 (chapter 7) on mating behaviour closely follows Perdeck's descriptions of nesting, courtship and copulation (Perdeck, 1963). Chapter 2 on numbers and distribution is a synthesis from many sources. The rest of the book is original. It describes the results of analyses of data from Fair Isle. I have already published a number of papers on the genetics, demography and sexual selection of the Arctic Skua analysing data for the period up to 1976. In this book, the data are now complete to the end of the breeding season in 1979. Chapters 9 and 10 are based on two published papers (O'Donald, 1980*b,c*), but extended with new theory and analyses. The data of chapter 4 on breeding ecology have never previously been published in any form. Some of our earlier conclusions on differences between pale and melanic males in the sizes of their territories (Davis & O'Donald, 1976*b*) have been contradicted by the subsequent data. In sections 7.3 and 7.4 (chapter 7), I analyse the complete data on territory size, finding no phenotypic differences, but a slight, statistically significant relationship of breeding date to territory size. In 1978 and 1979, my brother-in-law, Terry Lynch, assisted in the mapping of the nests and territories. He also took many photographs of Arctic Skuas, including those of the nest with eggs and the pale, intermediate and dark phenotypes of chicks which form figures 1.2, 1.4, 1.5 and 1.6. These are prints from colour slides.

In acknowledgement, I am most indebted to the Nature Conservancy, later the Natural Environment Research Council, first for the Research Studentship with which I began my career of research in population genetics, and then for the two Research Grants which supported the study of the Arctic Skuas in the period 1973–79. To all those who have helped me

Cambridge University Press

978-0-521-11334-2 - The Arctic Skua: A Study of the Ecology and Evolution of a Seabird

Peter O'Donald

Frontmatter

[More information](#)

xvi *Preface*

at various times – Peter Davis, John Davis, Roger Broad, Shoshana Ashkenazi, Jane French, Terry Lynch and Iain Robertson – I offer my sincerest thanks. Finally, I thank Miss Rena Beech who typed this book from my manuscript.