

T & A D POYSER

Bewick's Swan



EILEEN REES

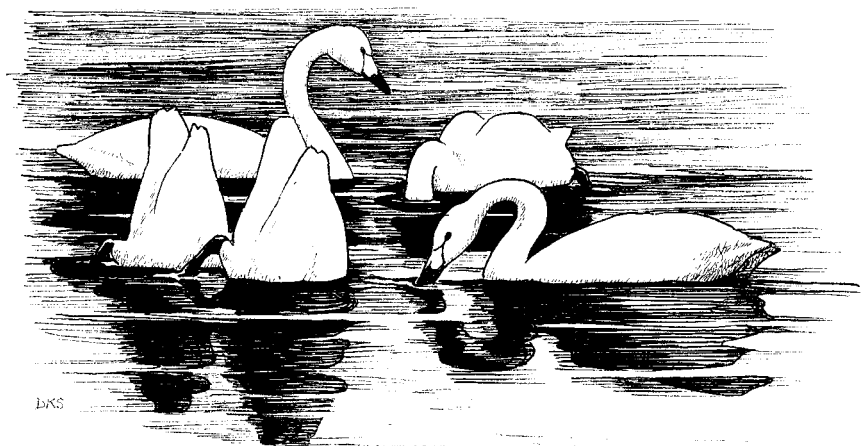
BEWICK'S SWAN

*For Val and Dewi,
and for
Peter and Phil*

BEWICK'S SWAN

EILEEN REES

Illustrations by
DAFILA SCOTT



T & A D POYSER
London

Published 2006 by T & A D Poyser, an imprint of A&C Black Publishers Ltd.,
36 Soho Square, London W1D 3QY

Electronic edition published 2010

www.acblack.com

Copyright © 2006 text by Eileen Rees
Copyright © 2006 illustrations by Dafila Scott

The right of Eileen Rees to be identified as the author of this work has been asserted by her
in accordance with the Copyright, Design and Patents Act 1988.

ISBN: 978-0-7136-6559-8
eISBN 978-1-4081-3310-1

A CIP catalogue record for this book is available from the British Library

All rights reserved. No part of this publication may be reproduced or used in any form or by any
means – photographic, electronic or mechanical, including photocopying, recording, taping or
information storage or retrieval systems – without permission of the publishers.

Commissioning Editor: Nigel Redman
Project Editor: Jim Martin

Typeset by Alliance Interactive Technology, Pondicherry, India

10 9 8 7 6 5 4 3 2 1

Contents

Acknowledgements	10
Preface	13
Chapter 1: SWANS AND THE BEWICK'S SWAN	15
1.1 SWAN TAXONOMY	18
1.1.1 <i>Comparison of Bewick's Swans with other swan species</i>	18
1.1.2 <i>Separation of Bewick's Swans from Whooper Swans</i>	19
1.1.3 <i>Separation of Bewick's Swans from Whistling Swans</i>	21
1.1.4 <i>Genetics studies</i>	24
1.2 BEWICK'S SWANS IN AVICULTURE	24
1.3 BEWICK'S SWANS: A CLOSER LOOK	25
1.3.1 <i>Sex and age differences</i>	25
1.3.2 <i>Geographic variation</i>	27
1.3.3 <i>Leucistic Bewick's Swans</i>	28
1.3.4 <i>Bill pattern variation</i>	29
1.3.5 <i>Heritability of bill patterns</i>	30
1.3.6 <i>Voice</i>	32
1.4 BEWICK'S SWAN STUDIES	32
1.4.1 <i>Early work (pre 1970)</i>	32
1.4.2 <i>Long-term studies at the Wildfowl & Wetlands Trust</i>	34
1.4.3 <i>Changing numbers and distribution in the vicinity of Wildfowl & Wetlands Trust reserves</i>	36
1.4.4 <i>Dutch Bewick's Swan studies</i>	38
1.4.5 <i>International collaboration</i>	39
Chapter 2: NUMBERS AND DISTRIBUTION	42
2.1 POPULATION SIZE AND TRENDS	43
2.1.1 <i>Western population</i>	43
2.1.2 <i>Eastern population</i>	46
2.1.3 <i>Caspian/west Siberian population and out-of-range sightings</i>	49
2.2 REASONS UNDERLYING CHANGES IN POPULATION SIZE	51
2.3 BREEDING DISTRIBUTION	52
2.3.1 <i>European Russia</i>	52

2.3.2	<i>Siberian Arctic</i>	54
2.3.3	<i>Historic changes in distribution across the breeding range</i>	59
2.4	MOULTING DISTRIBUTION	60
2.5	DISTRIBUTION IN WINTER	62
2.5.1	<i>Winter distribution: northwest European population</i>	63
2.5.2	<i>Winter distribution: eastern population</i>	74
2.6	STAGING AREAS AND NETWORKS OF KEY SITES	77
2.6.1	<i>Western flyway</i>	77
2.6.2	<i>Eastern flyway</i>	80
2.7	FACTORS AFFECTING SITE SELECTION IN WINTER	84
2.7.1	<i>Geographical location</i>	84
2.7.2	<i>Habitat</i>	84
2.7.3	<i>Interspecific competition with Whooper Swans</i>	86
Chapter 3: MIGRATION AND MOVEMENTS		88
3.1	MONITORING MIGRATION: RINGING PROGRAMMES AND OTHER TECHNIQUES	89
3.2	MIGRATION ALONG THE WESTERN AND EASTERN FLYWAYS	95
3.2.1	<i>Migration: northwest European population</i>	95
3.2.2	<i>Frequency of staging: northwest European population</i>	101
3.2.3	<i>Migration and frequency of staging: eastern population</i>	103
3.2.4	<i>Turnover and duration of staging</i>	104
3.2.5	<i>Migratory routes used by swans from different wintering sites</i>	107
3.2.6	<i>Variation in migration routes over time</i>	108
3.3	EFFECTS OF EXPERIENCE AND BREEDING STATUS ON ARRIVAL AND DEPARTURE PATTERNS	110
3.4	MIGRATORY TRADITION	112
3.4.1	<i>Site fidelity</i>	112
3.4.2	<i>Conflict within pairs regarding winter-site selection</i>	114
3.4.3	<i>Exploratory dispersal by sub-adult and single birds</i>	117
3.5	THE TIMING OF MIGRATION	119
3.5.1	<i>Importance of day-length in controlling migration</i>	119
3.5.2	<i>The effects of weather on migration patterns</i>	121
3.5.3	<i>Effect of body condition on migration patterns</i>	122
3.5.4	<i>Consistency in the migratory patterns of individual birds</i>	123
3.5.5	<i>Effects of dominance rank on migratory patterns</i>	125
3.6	OTHER ASPECTS OF MIGRATION	126
3.6.1	<i>Physical limitations</i>	126
3.6.2	<i>Orientation and navigation</i>	128

Chapter 4: FOOD AND FEEDING ECOLOGY	130
4.1 FEEDING HABITS	131
4.2 FOOD SELECTION	132
4.2.1 <i>Historical changes in winter diet</i>	132
4.2.2 <i>Changes in food selected during the course of winter</i>	133
4.2.3 <i>Feeding at migratory sites</i>	136
4.2.4 <i>Food selected in the breeding range</i>	137
4.2.5 <i>Occasional feeding on animal matter</i>	138
4.3 STRATEGIES WHEN FEEDING ON AQUATIC VEGETATION	138
4.3.1 <i>Intake of aquatic vegetation</i>	138
4.3.2 <i>Searching for food under water</i>	139
4.3.3 <i>Timing of switching between habitats</i>	139
4.3.4 <i>Effect of swan grazing on their food supply</i>	140
4.4 STRATEGIES WHEN FEEDING ON FARMLAND	141
4.4.1 <i>Movement between feeding areas during the winter</i>	141
4.4.2 <i>Variation in time spent feeding</i>	144
4.5 INDIVIDUAL DIFFERENCES IN FORAGING STRATEGIES	148
4.5.1 <i>Biases in feeding distribution for the different social classes</i>	148
4.5.2 <i>Feeding rates of parents and non-breeders</i>	148
4.6 ENERGY REQUIREMENTS	150
4.7 FEEDING COMPETITION OR COEXISTENCE	153
 Chapter 5: BREEDING BIOLOGY	 156
5.1 PAIR FORMATION	159
5.2 MATING	160
5.3 TIMING AND DURATION OF THE BREEDING SEASON	160
5.4 TERRITORIAL DEFENCE	161
5.5 PROPORTION OF BIRDS THAT ATTEMPT TO BREED	163
5.6 VARIATION IN BREEDING DENSITY	164
5.7 NESTING	168
5.8 RETURN RATES AND NEST-SITE FIDELITY	171
5.9 THE LAYING PERIOD	172
5.10 INCUBATION BEHAVIOUR	175
5.11 PREDATION	175
5.12 HATCHING	177
5.13 BROODS AND PARENTAL CARE IN SUMMER	178

5.14	CYGNET SURVIVAL	179
5.15	MOULTING PERIOD	181
5.16	WEATHER CONDITIONS AND BREEDING SUCCESS: A SYNTHESIS	182
5.17	BREEDING EXPERIENCE AND BREEDING SUCCESS: A SYNTHESIS	182
5.18	HABITAT AND OTHER FACTORS INFLUENCING BREEDING	184
5.19	OVERVIEW OF FACTORS AFFECTING BREEDING SUCCESS	185
 Chapter 6: SOCIAL BEHAVIOUR IN WINTER		 187
6.1	FLOCK STRUCTURE	187
6.2	DOMINANCE RANKS	188
6.2.1	<i>Aggressive encounters and other displays</i>	188
6.2.2	<i>Establishing dominance relationships</i>	192
6.2.3	<i>The importance of mate proximity in aggressive encounters</i>	194
6.2.4	<i>Costs and benefits of achieving social dominance</i>	195
6.2.5	<i>Maintaining dominance from one year to the next</i>	196
6.2.6	<i>Inheritance of dominance</i>	197
6.2.7	<i>Factors affecting social dominance</i>	197
6.2.8	<i>Timing of arrival and social dominance</i>	198
6.3	PARENTAL CARE IN WINTER	198
6.4	DISTRIBUTION OF INDIVIDUALS WITHIN THE FLOCK	200
6.4.1	<i>Roost distribution</i>	200
6.4.2	<i>Association between dominance and feeding distribution for birds from different roost groups</i>	201
6.5	SOCIAL BEHAVIOUR AND RETURN RATES	202
6.6	OVERVIEW OF RELATIONS WITHIN THE WINTERING FLOCK	203
 Chapter 7: LIFE-HISTORY STUDIES		 204
7.1	FIRST PAIRING	205
7.2	FIRST BREEDING	206
7.3	PAIR-BOND DURATION AND MATE FIDELITY	207
7.4	AN UNUSUAL ASSOCIATION	210
7.5	LONGEVITY AND SURVIVAL	211
7.6	LIFETIME REPRODUCTIVE SUCCESS	212
7.6.1	<i>Overall breeding success</i>	212

7.6.2	<i>Effects of mate change on individual breeding success</i>	214
7.6.3	<i>Pair-bond duration and breeding success</i>	217
7.6.4	<i>How reproductive success is affected by the combination of male and female characteristics, and the implications for mate choice</i>	218
7.7	IMPLICATIONS OF THE SWANS' LIFE-HISTORY STRATEGIES FOR SPECIES SURVIVAL	220
Chapter 8: THREATS AND CONSERVATION MEASURES		221
8.1	DIRECT THREATS TO THE SWANS: CAUSES OF MORTALITY	222
8.1.1	<i>Collisions with power lines</i>	223
8.1.2	<i>Illegal shooting</i>	224
8.1.3	<i>Disease and other causes of mortality</i>	225
8.2	THREATS TO SWAN SITES: HABITAT DEGRADATION AND POLLUTION	228
8.3	POTENTIAL CONFLICT: SWANS AND AGRICULTURE	230
8.4	CONSERVATION MEASURES	231
8.4.1	<i>National and international legislation</i>	231
8.4.2	<i>Site protection</i>	233
8.5	A VIEW OF THE FUTURE	234
Appendix 1.	<i>Winter weights and measurements of adult Bewick's Swans and Whistling Swans</i>	236
Appendix 2.	<i>Key staging and wintering sites for the northwest European Bewick's Swan population</i>	237
Appendix 3.	<i>Key staging and wintering sites for Bewick's Swans in the eastern population</i>	255
Appendix 4.	<i>Key staging and wintering sites for Bewick's Swans wintering in the Caspian region</i>	262
Appendix 5.	<i>Scientific names of plants and animals</i>	264
Appendix 6.	<i>List of abbreviations used in the text</i>	266
References		267
Index		293

Acknowledgements

In writing this book, I greatly underestimated the time that it takes to transfer thoughts to paper. I am therefore most grateful to the Wildfowl & Wetlands Trust, not only for the unique opportunity of studying Bewick's Swans in different parts of the world, but for tolerating the working hours spent on completing the manuscript during the final push to meet the final deadline. Meeting this deadline was greatly facilitated by encouragement from Valerie Rees, John Bowler and Chris Spray, who all took the trouble to read a full draft, and made a number of invaluable suggestions. John also kindly permitted use of data from his study of the swans' feeding ecology, which appear here in Chapter 4.

In addition to my mother, John and Chris, several other people made major contributions to one or more chapters. Wim Tijssen and Henk Schobben provided valuable information on individual swans seen in the Netherlands, including the story of Sligo and the Bean Goose in Chapter 7. Bart Nolet went through Chapter 4 in some detail; this section is greatly improved by his comments and published research. I am similarly indebted to Anna Belousova for her comments on the swans' breeding biology, to Kees Koffijberg for his updates on the numbers and distribution of Bewick's Swans in the Netherlands, to Axel Degen for information on the swans' use of key sites in Germany, to Simon Delany for his comments on population trends, and to Jan van Gils and Baz Hughes for their advice on Chapter 8. Konstantin Litvin kindly reviewed large parts of the text relating to Russia, and filled some of the many gaps in my knowledge of the Russian swan literature. I also thank Jan Beekman, Mennobart van Eerden, Trinus Haitjema, Marcel Klaassen and Richard Ubels for many enjoyable and fruitful discussions about Bewick's Swans over the years.

Stepping back to the start of the Bewick's Swan study at WWT Slimbridge, much of the credit for our current understanding of the Bewick's Swans can be attributed to the late Sir Peter Scott and his family. They initiated the detailed long-term study of individual birds at Slimbridge, which has since developed into a population study that extends along the swans' European flyway. In the early years, the individuals were recorded by Peter, his wife Philippa (who still takes a keen interest in the swans) and daughter Dafila. Dafila not only completed her doctoral thesis on the Bewick's Swans at WWT Welney (cited in Chapter 6), but has provided the line drawings which so greatly enhance the look of this book.

Several members of staff at Slimbridge have also been responsible for identifying the swans by their bill markings and, through their diligence and enthusiasm, have maintained the study for over 40 years. In chronological order, these are: Pat Pollard, Maya Scull, Tom Pitcairn, Mary Evans, John Bowler, Sue Carman and Julia Newth, with volunteer Steve Heaven also proving expert at swan identification. Each observer has been generous in training the next, thus ensuring the continuity of the study. I am personally indebted to Mary Evans for her training. Additionally, Jenny Earle maintains the Bewick's Swan database, and coordinates the network of people reading swan rings across Europe, assisted by volunteer Alison Bloor. Without the efforts of the ring-reading network and the swan

team at Slimbridge, there would be far less information on the Bewick's Swans, and this would be a much slimmer volume.

Other colleagues at WWT who have provided invaluable help, either with the Bewick's Swan study or with this book, include Linda Butler, Colin Butters, David Chamberlain, Sharmilla Choudhury, Ailsa Hurst, Nigel Jarrett, Robin Jones, Charlie Liggett, Geoffrey Matthews, Carl Mitchell, Malcolm Ogilvie, Kevin Peberdy, Dave Paynter, Mark Roberts, David Salmon, Darrell Stevens, Chris Tomlinson, the staff members that have fed the swans and all those who have helped at swan catches. Ruth Cromie and Martin Brown corrected sections on animal health in Chapter 8. Janet Kear not only participated in the Bewick's Swan study in its early years, but subsequently gave regular encouragement to the author, and I remain indebted to her.

For their comments and advice on various topics I am grateful to Linda Birch, Helmut Eggers, David Gardner-Medwin, Marcel Klaassen, Colin Pennycuick, Christopher Perrins, Dewi Rees, Jevgeni Shergalin, Mike Smart, Pat Smiddy and Mike Wilson. David Parkin and Nick Harvey kindly took the trouble to explain results of their studies on swan population genetics. I also thank Jeroen Nienhuis for further information from the Netherlands; Bjarke Laubek and Einar Flensted-Jensen for information from Denmark; Koen Devos, Ekhart Kuijken and Christine Verscheure for swan counts from Belgium; Fabrice Croset for data from France; Graham McElwaine for updates from Ireland; Saulius Švažas and Maria Wieloch for information from Lithuania and Poland respectively; and Leho Luigujõe and Andres Kuresoo who, with Taivo Kastepold and the late Valdur Paakspuu, have ensured that we are aware of the swans' key staging sites in Estonia.

One of the joys of the Bewick's Swan study in recent years has been the excellent communication with Russian scientists, both in exchanging information and in undertaking joint expeditions to the swans' breeding grounds in arctic Russia. Initial information became available through the pioneering work of Yuri Mineyev, who has been studying Bewick's and Whooper Swans in European Russia since the 1970s. Evgeny Syroechkovski Jnr. has not only recorded recent breeding distribution in Chukotka but, since 1995, has ensured that the work of his compatriots is published regularly in the Bulletin of the Goose Study Group of Eastern Europe and Northern Asia (*Casarca*). I thank him for his communication and cooperation. I am especially grateful to friends and co-workers from the All-Russian Research Institute and from the Nenetskiy State Nature Reserve for ensuring that the joint studies undertaken within the reserve are not only fruitful but a delight. In particular I thank Anna Belousova, Yuri Morozov and Andrei Glotov for their valued friendship. I also thank Sergei Mukhortov and the staff at the Nenetskiy State Nature Reserve, Nicolai Kotkin, and the late Sergei Petrushenko for their help during expeditions to the Russian arctic. Of key importance was Yuri Shchadilov who, although sadly no longer with us, was instrumental in developing the long-term study of Bewick's Swan breeding biology undertaken by WWT and the All-Russian Research Institute. Several other people have provided useful information from other parts of Russia, including Konstantin Litvin (Vaygach Island), Tatjana Hochlova (Karelia), Vladimir Borisov (Pskov region), and Vladimir Pozdnyakov (Lena Delta), and I am most grateful to them.

This book is biased towards the northwest European Bewick's Swan population, although the eastern population has received increasing attention in recent years. Sections on the latter would have been even lighter without input from Mark Barter and Ma Ming (for China), Nial Moores (for Korea), and John O. Albertsen, Mark Brazil and Yoshi Miyabayashi (for Japan); I am most grateful to them for letting me know about the swans' eastern flyway. Even

less is known about the swans wintering in the Caspian region, but Eldar Rustamov has provided counts from Turkmenistan, which have added to the pool of knowledge about the swans wintering in this area.

The Bewick's Swan research and conservation programme at Slimbridge is supported by the Wildfowl & Wetlands Trust, and I thank WWT, its Members and those that have joined the WWT Swan Adoption Programme for their contribution over the years. Fieldwork in Russia has been supported by, in chronological order: the Winston Churchill Memorial Trust, the Royal Society, British Airways Communities and Conservation, the Peter Scott Trust for Education and Research in Conservation, and the BBC Natural History Unit (Radio). The BBC (notably Julian Hector) not only supported the satellite tracking of Bewick's Swans from Russia in 2003, but Brett Westwood and Simon Roberts (BBC) and Colin Pennycuik (Bristol University) proved entertaining members of the expedition to Russia that year.

I am extremely grateful to Andy Richford for his original interest in a book on the Bewick's Swan, to Jim Martin at T & A D Poyser for seeing it through to publication, and to editors Tim Harris and Wendy Smith. It is also a pleasure to thank James McCallum for his evocative portrayal of the swans in the cover illustrations. The American Ornithologists Union, the Association of Animal Behaviour, *Ardea*, *The Auk*, the British Ecological Society, British Ornithologists' Union, the BTO, the Waterbird Society, Wetlands International, and the Wildfowl & Wetlands Trust all kindly granted permission to reproduce figures first published in their journals. Additionally, the photographs taken by Mark Barter, Mariusz Blank, Joe Blossom, John Bowler, Mark Brazil, Andrew Cooper, Mark Hulme, Paul Marshall, Dave Paynter, Philippa Scott and Wim Tijsen portray the beauty of the swans better than any words.

Finally, I thank Ronald Graham, not only for useful comments on the text, but particularly for his tolerance of the many weekends spent writing this book, and for his constant support and encouragement during a lifetime's study.

Preface

Each autumn, as the snow returns to the High Arctic, thousands of Bewick's Swans fly south to their wintering haunts in northwest Europe and east Asia. In Russia there is an old saying, *Lebed' nesyt sneg na nosu*, which means 'the swan brings snow on its bill'. Yet despite the colder weather their arrival is eagerly anticipated by birdwatchers and the wider public in countries ranging from Ireland to Japan. The first few birds may appear singly or in family groups but, as winter sets in, "swanfalls" of tens or even hundreds of Bewick's Swans arrive in waves to delight those who watch them with their grace, beauty and melodious calls.

At the Wildfowl & Wetlands Trust at Slimbridge in southwest England, there is additional interest in the swans' return. Here the life-histories of individual Bewick's Swans have been studied since the early 1960s, and the latest news of old friends – whether they have survived the migration, found a mate or raised young – is eagerly anticipated. The long-term study of the Slimbridge-wintering flock has provided substantial insight into the behaviour, ecology and dynamics of the species. More recent studies in other parts of the swans' migratory flyway have emphasised the range of environmental conditions that they encounter at different times of the year. This book aims to draw together the results of these studies to describe the many and varied aspects of the lives of these elegant birds, including threats to their welfare and the conservation measures introduced over the years.

The swans are the stars of this book, but there are also many untold human stories behind our current knowledge of the swans' lives. The acknowledgements go only a small way to show the dedication of people involved in the research, management and conservation of Bewick's Swans in very different parts of the world. As long ago as 1875, the Victorian naturalist and explorer Henry Seebohm made a remarkable journey by train, sledge and boat to the delta of the Pechora River in the Russian arctic. There he found Bewick's Swans nesting in what remains an important breeding area for the species to this day. Another eminent naturalist, Sir Peter Scott, claimed the Bewick's Swan as his favourite bird when, in February 1964, wild swans wintering on the saltmarshes at Slimbridge started visiting the lake in front of his house. Having previously favoured Pink-footed Geese, then Red-breasted Geese and Lesser White-fronted Geese, Sir Peter became fascinated by the migratory swans which he and his family found that they could recognise as individuals by the unique variation in their black-and-yellow bill markings.

My own involvement came much later – WWT's long-term study was in its 15th winter by the time I joined in 1977. Despite having to check prior to my interview in Myrfin Owen's book *Wildfowl of Europe* to determine what a Bewick's Swan was, in the first of many winters studying the birds I fell immediately for their fidelity (both to their families and to particular wintering sites) and delicate beauty. Although now based at WWT Martin Mere – a stronghold of the larger Whooper Swans – watching the Bewick's Swans sweep in at dusk to feed, preen and roost on Swan Lake at Slimbridge inspires great joy and contentment during my weekly visits to WWT's headquarters. Ornithologists elsewhere have similarly

fallen under their spell, with those involved in ring-reading – particularly the Dutch ring-readers – travelling widely to track the movements of colour-ringed swans during winter and the early stages of spring migration. In Japan, where the swans are much admired, supplementary food has been provided at an increasing number of sites over the last 50 years, and visiting these sites continues to be very popular with the general public.

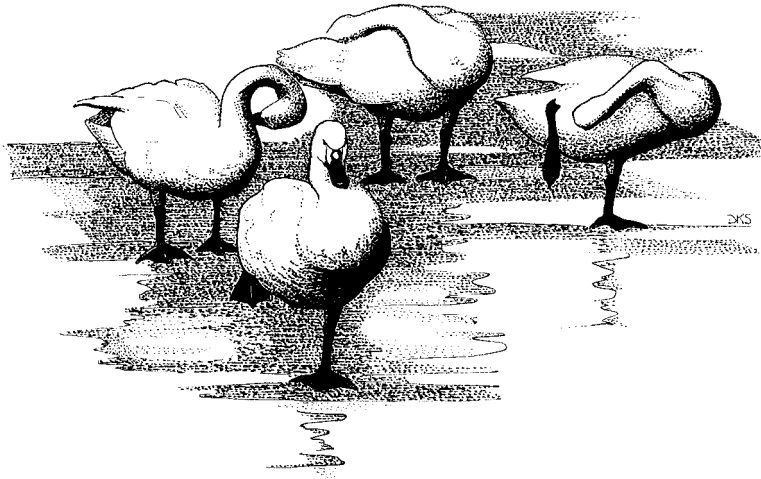
Expeditions to the swans' breeding grounds on the Russian tundras are now a little easier than in Seeböhm's time. Nevertheless they pose some new challenges and have only been open to western scientists since the end of the Cold War. It is now possible to fly from Moscow via Arkhangelsk to Nar'Yan Mar on the Pechora Delta, and on clear days the views of the vast tundra landscape along the arctic coastline is truly a wondrous sight. The helicopter from Nar'Yan Mar to the swans' breeding areas passes over a myriad of lakes, channels and small pools, which not only provide breeding territories for the swans but are used by the many other wildfowl and waders that live on the tundra during the summer months. Clouds of mosquitoes, the bane of researchers, provide food for many bird species in both larval and adult forms. Fish, the main food of researchers, are netted in adjacent waters.

In 2003 we gained permission from the Radiofrequency Centre in Moscow to deploy satellite-transmitters on five Bewick's and one Whooper Swan to monitor their autumn migration, the first time that the use of such transmitters has been officially permitted in Russia. The satellite-tracking programme was a major feature in BBC Radio 4's migration week, and generated widespread interest in the swans and their welfare. Education programmes and media coverage within Russia similarly aim to inspire the next generation with an interest in the birds and their habitats, which is essential for safe-guarding their future as man encroaches into their remote breeding grounds.

Since migrant birds are no respecters of political boundaries, effective conservation requires not only sound knowledge of their ecological requirements throughout the year, but also the political will in countries throughout their range to introduce appropriate conservation measures where necessary. Therefore, the designation of the swans' breeding grounds north of the Pechora Delta as a National Nature Reserve (the *Nenetskiy zapovednik*) by the Russian Government in 1998 was particularly satisfying to all concerned. The expansion of the Bewick's Swan study, from focusing on the swans wintering at Slimbridge to studies at their migration sites and breeding grounds, and the development of research programmes by scientists in other countries, has greatly improved our understanding of their lives.

Although our knowledge of the swans has increased substantially since the early 1960s, gaps do still remain. Thus, both for myself and for others delighted by these beautiful birds, what commenced as a study of the swans' lives may well become a lifetime's study.

Eileen Rees
WWT Martin Mere, November 2005



CHAPTER 1

Swans and the Bewick's Swan

'The name of those fabulous animals (pagan, I regret to say) who used to sing in the water, has quite escaped me.' Mr George Chuzzlewit suggested 'Swans'. 'No,' said Mr Pecksniff. 'Not swans. Very like swans, too. Thank you. ... Wait. Sirens! Dear me! Sirens, of course.'

Charles Dickens (*Martin Chuzzlewit*)

Of all the species of bird on this planet, the Bewick's Swan *Cygnus columbianus bewickii* must be one of the most appealing. It starts with an unfair advantage over many other species simply by being one of the swans, birds whose grace and pure beauty has been the subject of legends and fairy tales since the dawn of time. It then steals a march over the magnificent but more sedentary Mute Swan *Cygnus olor* by being migratory, which adds greatly to its mystique. The Bewick's Swans' summer haunts on the High Arctic tundra are still largely inaccessible, so few people have the good fortune to follow them on their long-distance journeys to their nesting areas. Next, it is the smallest and most delicate of the northern migratory swans, even more delicate than its close relation the Whistling Swan *Cygnus columbianus columbianus*, which occupies the same ecological niches in North America as those used by the Bewick's Swan across Eurasia. Not only are Bewick's Swans beautiful – they are also musical. The concept of the 'silent swan', which sings only just before death, is probably based on the Mute Swan; in fact the Mute does vocalise but through inelegant snorts and grunts. It clearly does not refer to the Bewick's Swans, which bugle loudly during territorial disputes and utter gentler crooning or contact calls to their mates and offspring. Then there is the birds' life-style – their faithfulness to their mates and care of their young are reminiscent of another species that is long-lived with slow-growing offspring – mankind. Yet although the swans have generally delighted humans over many

years, we will see here that human activity has had major costs as well as some benefits to the species.

Studies of individual animals are immensely rewarding, not only for the quality of the scientific findings, but also on a more personal level for the researchers involved. The value to science and conservation lies in the fact that differences in behavioural patterns are often associated with characteristics (such as age, sex, dominance and breeding success) of the individuals concerned; these in turn help to explain how or why animals behave as they do. Individual-based studies are being used increasingly to explain and predict changes within populations, and particularly the reasons and processes underlying changes in population size and shifts in distribution. Knowledge of the individuals' life histories is especially valuable in this detective work, since in many cases the behaviour is related to their past experiences. Thus, breeding success may be influenced by the length of time that members of a pair have been together, or by their familiarity with the breeding territories, or by the number of offspring raised the previous year. The subtleties of the ways in which animals relate to each other and to their environment are less easily understood by monitoring 'unknown' individuals, even when these are part of a group, because relevant information may be lacking. Nevertheless, zoologists thinking of embarking on a study of individual animals should maybe think twice about doing so. Not only will many years of work be required to obtain useful information about a species if it turns out to have a long lifespan, but detailed studies often lead to new ideas that stimulate further research. Moreover, the level of involvement can result in an increasing concern for the welfare of the individuals being monitored, who can become old friends over the years. This has certainly been the case with the Bewick's Swan. Almost all those who have started studying the species have ended up doing so for five years or more. Although the author joined the long-term study of Bewick's Swans' life-history strategies on a temporary contract in 1977, it now seems to be becoming a lifetime's undertaking.

It all started in a very small way, when the eminent naturalist and conservationist Sir Peter Scott had the idea of attracting to the lake in front of his house the small flock of wild Bewick's Swans which wintered on the River Severn at Slimbridge in Gloucestershire. Swans are gregarious except when breeding so, during the 1963–64 winter, seven conspecifics (three Bewick's and four Whistling Swans) from the collection of captive birds at the Wildfowl Trust (now the Wildfowl & Wetlands Trust, WWT) were put on the lake, in the hope that wild swans would be decoyed from the river by their calls. The ploy was entirely successful. By the end of the winter the 24 wild swans present on the estuary were visiting the lake regularly, where they could be observed closely from buildings and hides. The Scott family immediately took a keen interest in the new arrivals in front of their studio window, and quickly realised that the birds could be told apart by differences in their black-and-yellow bill patterns. Moreover, when the swans arrived at Slimbridge the following winter, the Scotts found that they could recognise some individuals that had been present the previous season, in some cases accompanied by their new mates and offspring. This ability to identify individuals by their natural markings, together with the swans' tendency to return to the same sites over several winters, formed the basis for a long and detailed study of the species. Initially, observations centred on the swans wintering at Slimbridge, but the study expanded with a view to monitoring the same birds at other wintering sites and along their migratory route to the northern wintering grounds, in collaboration with scientists from other parts of northwest Europe.

Even Sir Peter may not have realised the extent to which the monitoring of individual swans would develop into a long-term study, due at least in part to the swans' long lifespans. Although the Slimbridge study has been underway since February 1964, the longevity of the birds means that even after 30 years we still do not know some elementary facts, such as their potential life expectancy. A swan named 'Casino' returned to Slimbridge for her 27th winter at the site in 1997–98, looking fit and well and accompanied by her six-year-old offspring 'Croupier'. Since she was first recorded as a cygnet in 1971, Casino was 26 years old at the time. Eleven more birds have reached at least 25 years of age in the wild and, at the time of writing (autumn 2005), 68 have been recorded at 20 years or more. One captive swan, named 'Mrs Noah', was at least 33 years old when she died at Slimbridge, apparently of old age. New benefits of long-term data from both individual and population studies are coming to light, however, which may be used to explain and predict population changes associated with changes in habitat and climate over several years or decades. Thus, information on the feeding habits of the swans during the 1960s and 1970s, compared with more recent observations, show that the swans' diet has also changed over time in response to habitat loss and changes in farming practice. Such evidence, which is invaluable for monitoring the ability of populations to adapt to environmental changes, can only be obtained by monitoring a species systematically over long periods of time.

Although the Bewick's Swan study at Slimbridge was the first to study the species in any depth, scientists at other sites along the swans' migratory route from northwest Europe to Arctic Russia have embarked on separate and collaborative projects, which have added substantially to our knowledge and understanding of the swans' life-cycle. Amateur and professional ornithologists in the Netherlands originally became involved in Bewick's Swan research due to their concern following the disappearance of aquatic vegetation at the swans' feeding sites in the IJsselmeer area during the 1960s, which resulted in the birds changing to feed on farmland (Poorter 1991). The marking of Bewick's Swans with leg-rings since the late 1960s also engaged Dutch ring-reading enthusiasts, who continue to spend much of their valuable leisure time during the short winter days in reading the swans' ring codes and reporting their sightings. The initiation of the Dutch Bewick's Swan study in 1982 resulted in the development of a new long-term study of the species, which is still underway and expanding. The Netherlands is the most important wintering area for the species in Europe, and Dutch colleagues have been responsible for coordinating the international Bewick's Swan censuses across Europe, made every five years since the first 'complete' census of 1986. This is particularly valuable for monitoring total numbers within the population and for verifying the population trends derived from annual counts at selected sites, including those sent to Wetlands International (previously the International Waterfowl and Wetlands Research Bureau) as part of their international waterfowl counts programme.

The intensive studies of Bewick's Swan, not only by the Wildfowl & Wetlands Trust but increasingly by scientists at other sites along its European flyway, means that our insight into the life of this beautiful bird is very comprehensive. Comparisons of the results obtained in Britain, the Netherlands and at migratory sites in Estonia emphasise the importance of not restricting research to a single area or to just one season. Differences in the food selected, for instance, indicate either that the swans' ecological requirements change throughout the year, or that they are adapted to the conditions in which they find themselves, as indicated in Chapter 4. The opportunity for Western Europeans, used to seeing Bewick's Swans only in winter, to join Russian scientists in studying the birds at their nest

sites on the tundras of Arctic Russia revolutionised our view of the birds, because the swans' habitat and behaviour is so totally different in the breeding season. Less is known about the eastern population, which migrates from the Arctic tundras of far eastern Russia to winter in Japan, China and Korea, but greater international communication and collaboration is also helping to fill in these gaps in our knowledge. This book therefore aims to draw together the substantial volume of information gained about Bewick's Swans over the years, to describe and explain the varied aspects of the swans' migrations and life histories and, it is hoped, to provide the reader with greater insight into the remarkable life of the Bewick's Swan.

1.1 SWAN TAXONOMY

1.1.1 *Comparison of Bewick's Swans with other swan species*

Swans need very little introduction. Their large size, long necks, short legs and large webbed feet make them amongst the easiest of all birds to recognise, familiar to most people except perhaps in Africa where only a few hundred feral Mute Swans are to be found in the southern part of the continent. Taxonomists appear to be united in considering that waterfowl, consisting of the swans, geese and ducks, belong to one family, the Anatidae. Classification of members of the Anatidae family into genera, species and subspecies is still being debated, however, including the number of swan genera and species thought to exist. The most widely held view is still that of Delacour & Mayr (1945), who considered that there are eight species or subspecies of swans in the world, five in the northern hemisphere and three in the southern hemisphere. They are also classified as falling within two genera since one species, the Coscoroba Swan *Coscoroba coscoroba* from South America, is so distinctive that it has been allocated its own genus. Indeed, the question of whether it is truly a swan is still under investigation. The seven other species or subspecies are currently grouped together in the *Cygnus* genus, although the Eurasian Mute Swan, the Black-necked Swan *Cygnus melanocoryphus* from South America and the Black Swan *Cygnus atratus* from Australia (introduced to New Zealand in the 19th century, Bowler 2005a) clearly differ from the northern migratory swans, both in physical appearance and in their behaviour patterns (Kear 2005). The Mute Swan, like the other northern hemisphere swans, has white plumage in adulthood but can be readily distinguished by its reddish-orange bill with a black knob at the forehead, the graceful curve to its long neck and the longer upturned tail. The Black-necked Swan, as its name suggests, has a striking black head and neck on a white body, with a red caruncle at the base of the bill. The Black Swan has predominantly black or near-black plumage with a bright red bill and eyes; white primary feathers and distal secondary feathers are visible in flight.

Trumpeter Swans *Cygnus buccinator*, Whistling Swans, Whooper Swans *Cygnus cygnus* and Bewick's Swans, known collectively as the northern migratory swans, are thought to be more closely related to each other than to the other swan species. They are similar in physical appearance, with the adults having all-white plumage, an upright stance with necks held rather straight, and varying amounts of black and yellow on the bill. Unlike the Mute and Black-necked Swans, they do not have a frontal knob or caruncle at the base of the bill. Also, unlike the Mute Swan and Black Swan, they do not arch their wings in aggression, but perform a series of ritualised displays, raising and flapping their wings and calling loudly. Trumpeter and Whistling Swans breed across the sub-Arctic

and Arctic regions of North America respectively, in areas analogous to the breeding distribution of Whooper Swans and Bewick's Swans in Eurasia. All four species migrate south in autumn/winter to more temperate latitudes. The ranges of Bewick's and Whooper Swans overlap, particularly in winter, but Bewick's x Whooper hybridisation has never been recorded in the wild. Trumpeter and Whistling Swans are less likely to be found at the same sites, probably due to the somewhat limited distribution of the Trumpeter Swan, following a drastic reduction in numbers due to excessive hunting in the 19th century.

The Bewick's Swan is the smallest of the northern swans, and arguably the smallest of all swans depending on how the Coscoroba Swan is classified. Bewick's Swan's relationship with the nominate *Cygnus columbianus columbianus* is still unclear, with some authorities considering Bewick's and Whistling Swans to be two separate species (for example, Stejneger 1882, Wetmore 1951, Vaurie 1965), whereas others believe them to be conspecific but different subspecies (Hartert 1920; Delacour & Mayr 1945; Parkes 1958; Mayr & Short 1970). The inclusive name Tundra Swan was suggested by Palmer (1976) for both Bewick's and Whistling Swans, and this term has been commonly used for the Whistling Swan in North America from the 1980s onwards. There have been increasing moves towards referring to Bewick's Swans as Tundra Swans in Europe in recent years, and in 2004 the British Ornithologists' Union recommended that Bewick's and Whistling Swans should be treated as conspecifics (Sangster *et al.* 2004). Biometric data recorded for Bewick's and Whistling Swans indicate that the latter is generally larger, but that the body weights and measurements do overlap considerably (Appendix 1). Moreover, there are few measurements of Bewick's Swans from the easternmost parts of their range, where hybridisation with Whistling Swans occurs. The overlap of the Bewick's and Whistling Swans' breeding ranges in far east Russia, and sightings of mixed pairs and hybrids since the 1970s, confirms that interbreeding does occur in the wild, although its frequency is still not known. This is a major reason for grouping Bewick's and Whistling Swans as a single species, despite the obvious visual differences in their bill markings.

It has been suggested that birds from the eastern Bewick's Swan population have larger bills, broader near the tip and higher near the base than those further west, and with slightly more yellow on the bill. Whether they should be described as a separate race (known as Jankowski's Swan *Cygnus columbianus jankowskii*, Alphéraky 1904; or *Cygnus c. bewickii jankowskii*, Delacour 1954) therefore has been debated, but Bewick's Swans have long been classified as a single group, with populations that follow different migration routes not divided taxonomically. There is substantial variation in the skull and bill measurements of swans from the western population, and the few records obtained for the eastern population (notably the bill lengths of four adults and two cygnets received by the Wildfowl Trust from Hong Kong in 1973) fall within this range. The bill patterns of six '*jankowskii*' swans at the Wildfowl & Wetlands Trust also appeared typical for *bewickii* (Evans & Sladen 1980). Given that differences in body size have been recorded for other bird populations that have not then been described as different races (for example, Whooper Swans and some of the goose populations), it remains difficult to justify separating Jankowski's Swan on the basis of its size alone.

1.1.2 Separation of Bewick's Swans from Whooper Swans

Bewick's Swan is named after the famous 18th-century engraver and ornithologist Thomas Bewick of Newcastle, who died in 1828 two years before the bird was described in print. It is one of the last large birds occurring in Britain to have been recognised and named by the

scientific community, having previously been classed together with Whooper Swans as 'Wild Swans'. That this group included some smaller birds (which he recognised as a 'variety' rather than a separate species) was first noted by Pallas in 1811. In 1824, John Latham again mentioned a 'Lesser Swan ... not so large as the Hooping Swan ... in fact, it imitates the Wild Swan in miniature...'. Latham had only a single skin, however, so he was unwilling to propose it as a distinct species. The breakthrough came in October 1829, when Richard Wingate (a taxidermist from Newcastle) presented a paper to the Natural History Society of Northumberland, Durham and Newcastle upon Tyne (now The Natural History Society of Northumbria) which described Bewick's Swan in detail but failed to give it a name. Between June and October 1830, his friend P.J. Selby published a paper in the Society's *Transactions*, naming the swan as 'Cygnus Bewickii of Wingate' and acknowledging the help of Sir William Jardine and William Yarrell. Meanwhile, Yarrell wrote another account of the new species, which was published in the *Transactions of the Linnean Society* in the same year (Yarrell 1830), in which he 'proposed to call it Bewick's Swan, thus devoting it to the memory of one whose beautiful and animated delineations of subjects in natural history entitle him to this tribute'. Because Yarrell's paper was published a couple of months before Selby's, Yarrell is usually credited with describing Bewick's Swan. He did not claim to be aware of the Bewick's Swan first, but he did say in January 1830 (and wrote in his paper) that he had suspected the new species on the basis of the characteristic anatomy of the trachea, bronchi and sternum in a specimen prepared 'six years ago' (i.e. about 1824); his first spoken declaration of this was in November 1829, a month after Wingate (D. Gardner-Medwin pers. comm.). This may have caused some bad feeling at the time, but all parties clearly were happy with the choice of name. It is not known whether Bewick ever saw the bird to which his name was given, but his telescope (dated 1794) has been used for watching Bewick's Swans at Slimbridge. His son, Robert Elliot Bewick, engraved an image of a Bewick's Swan for the 1847 posthumous edition of his father's *The History of British Birds* (D. Gardner-Medwin pers. comm.).

In the field, Bewick's Swans are more likely to be confused with Whooper Swans than with any of the other swans because they are superficially similar in appearance and their ranges overlap. The Bewick's Swan is smaller and more goose-like in flight, however, with a comparatively shorter-looking neck and a more rounded head; Whooper Swans tend to have a flatter profile of the bill and head. The easiest way to tell the two species apart, at least for yearlings and adult birds is by the distribution of the yellow and black markings on the bill. In Bewick's Swans the yellow markings at the base of the bill end behind the nostrils, whereas in Whooper Swans the yellow extends to a point beyond the nostrils, giving the yellow pattern a wedge-like appearance. Bill patterns cannot usually be used to differentiate between Bewick's and Whooper Swans for birds in their first winter, although emerging bill markings may be seen at close quarters towards the end of the winter season, but differences in the overall body structure and head shape are apparent after fledging. The grey plumage of Whooper Swan cygnets wintering in Britain tends to become whiter more rapidly than that of Bewick's Swan cygnets, perhaps indicating that they mature more rapidly. Large variation in cygnet plumage between broods and the darker grey feathering observed in Finnish-bred Whooper Swans seen wintering in Britain, however, indicate that other factors (e.g. diet) may also be involved. Some Bewick's Swans retain traces of the juvenile grey feathering on the head and neck into their third summer (J. Beekman pers. comm.), whereas many Whooper Swans have all-white adult plumage at one year old (second summer). The calls of the two species also differ, although both are highly vociferous. Bewick's

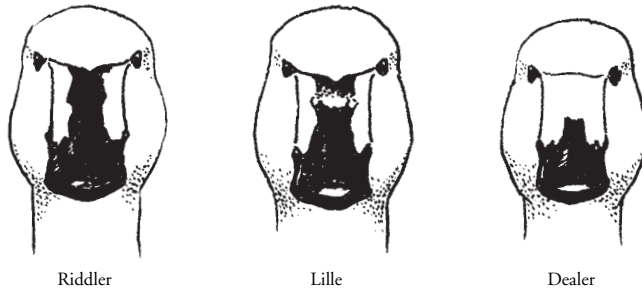


Figure 1.1 Illustration of variation in bill patterns of Bewick's Swans, showing the three main types: blackneb (Riddler), pennyface (Lille) and yellowneb (Dealer).

Swans generally make higher pitched and more musical notes than the more sonorous whooping calls of the Whooper Swan.

1.1.3 *Separation of Bewick's Swans from Whistling Swans*

Although Bewick's Swans are slightly smaller on average than Whistling Swans, the most reliable field characteristic for distinguishing between adults of the two subspecies is the proportion of yellow on their bills. Their body shape and posture are very similar, as are their calls (the position of the trachea within the sternum being the same for both), but experienced aviculturalists can differentiate between their voices at close range (N. Jarrett and M. Roberts pers. comm.). In Whistling Swans the bill is almost entirely black in colour, but usually with a small and variable patch of yellow in front of the eye. In Bewick's Swans the proportion of yellow is much larger, in some individuals (known as 'yellownebs') stretching in a continuous band across the bill to link the yellow patches on either side. In other Bewick's Swans (known as 'blacknebs') the centre-line of the upper mandible is black from the feathering to the tip of the forehead, and in a third group ('pennyfaces') the front of the bill is black from the brow-line to the tip, but a patch of yellow (the 'penny') occurs in the middle (Scott 1966; Evans 1977a; Rees 1981; Figure 1.1).

A comparison of photographs taken of the right bill profiles for Whistling Swans caught in the eastern part of their North American range (where hybridisation with Bewick's Swans is least likely) and for Bewick's Swans caught at Slimbridge showed that the average proportions of yellow to the whole bill profile were 3.1% for Whistling Swans ($n = 300$) and 31.5% for Bewick's Swans with blackneb bill patterns ($n = 104$) (Evans & Sladen 1980). Nine Whistling Swans (3% of the sample) had no yellow patch at all. The largest proportion of yellow recorded for the Whistling Swan bills was 15.8%, and the smallest proportion of yellow recorded for the Bewick's Swan bill was 22.9% (Figure 1.2). Thus the ranges appeared to be discrete, giving greater credibility to out-of-range sightings for the two species and also to records of intergrades.

The amount of yellow on the bill therefore has been used to support reports of Bewick's and Whistling Swans seen outside their normal ranges (reviewed in Evans & Sladen 1980). Generally, Whistling Swans breed on the tundras of North America and migrate south each autumn to spend the winter in California (the western population) and in Delaware, New Jersey, Maryland and Virginia (the eastern population), whereas Bewick's Swans breed in the Russian Arctic and winter mainly in northwest Europe and east Asia (see Chapter 2). Photographs of the bill patterns confirmed that three Whistling Swans or Whistling x Bewick's Swan intergrades occurred in the normal range of Bewick's Swans, and that

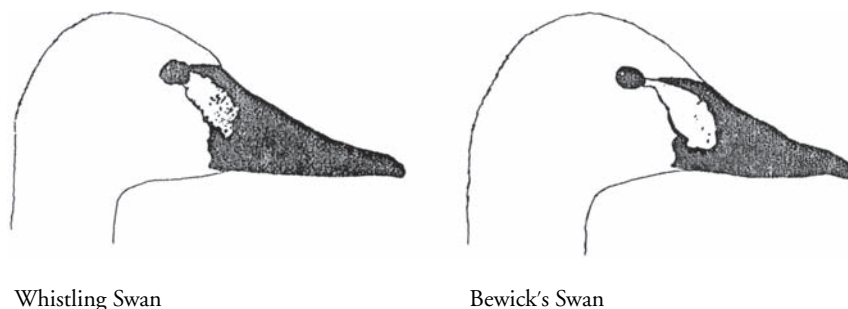


Figure 1.2 Comparison of the proportions of yellow to black on the bills of Bewick's and Whistling Swans. The Whistling Swan shown was the one with most yellow (15.8%) on its bill (left), and the Bewick's Swan was the one with the least yellow (22.9%). Bill patterns traced from photographs. From Evans & Sladen 1980.

four Bewick's Swans or Whistling x Bewick's intergrades occurred in the normal range of Whistling Swans during the 1980s. These consisted of two Whistling Swans seen in Japan, one Whistling Swan (or possibly an intergrade; 15.3% of yellow on the bill) in England, three Bewick's Swans in North America (in Maryland, Oregon and Saskatchewan) and a Whistling x Bewick's Swan intergrade (with 17.8% yellow on the bill), also seen in Canada. One of the Bewick's Swans seen in North America (in the Lower Klamath National Wildlife Refuge at Worden in Oregon) had a Whistling Swan mate and a family of two cygnets. A group consisting of a Bewick's Swan with Whistling Swan mate, three immatures (thought to be Bewick's or Bewick's x Whistling intergrades) and two other adults (possibly intergrades) seen on Hog Lake, near Red Bluff, California, the following winter may have been the same family party, but unfortunately photographs of the birds were not detailed enough to confirm their identities. A further out-of-range report was supplied in December 1977 when a Bewick's Swan marked with an orange neck-band was found dead at Adak Island in the Aleutian Islands, Alaska. The bird had been caught and marked as a cygnet in Chaunskaya Bay in northeast Siberia by A. Y. Kondratiev and other Soviet scientists as part of the USA-USSR Environmental Protection Agreement (Evans & Sladen 1980).

Most out-of-range reports of Bewick's and Whistling Swans have not had the benefit of photographic evidence, particularly the earlier sightings. Although photographs are an extremely useful diagnostic tool, the proportion of yellow on the bill can only be determined for certain by photographing the bill at right angles to the camera, in conditions free from shadow and when there is no mud (or, in one case, oil) on the bill, requirements that are difficult to achieve for swans in the field. Nevertheless, Whistling Swans appear to have occurred as vagrants in northeast Siberia since the second half of the 19th century, with sightings from Bering Island as early as 1882 and Novomarinisk (currently Anadyr) in 1897 (Dementiev & Gladkov 1952). More recently, a pair with three cygnets and five other Whistling Swans were discovered at Kolyuchin Bay on the Chukotka Peninsula in July 1974 (Kishchinski *et al.* 1975). There was a general increase in Whistling Swan numbers at Kolyuchin Bay during the mid 1970s to 1980s, and some 600–1,000 birds are now thought to occur in Chukotka in summer (Syroechkovski 2002; Chapter 2). A mixed Bewick's x Whistling Swan pair was seen on the Ekviatap estuary (179°E) in 1990, although a nest was not found (M. S. Stishov pers. comm., in Syroechkovski 2002).

In the southern part of the flyway, between 10 and 29 Whistling Swans have been observed at Bewick's Swan wintering sites in Japan each year since 1990 (Environment Agency

of Japan 1998). A mixed Bewick's x Whistling Swan pair was seen in Japan in the 1970s (T. Ohmori pers. comm., in Evans and Sladen 1980), and there were a further four reports of mixed pairs in Japan in the late 1980s, including a family with two cygnets (Mikami 1989). In addition to the mixed family party seen for one or two years in Oregon and California, an adult Bewick's Swan accompanied by an immature was seen in California in February 1975 (Stallcup & Winter 1975), three possible Bewick's x Whistling Swan intergrades on Victoria Island, California, in the 1977–78 winter and another possible intergrade near Benton, California. A Bewick's Swan (identity confirmed by photographs) seen in Saskatchewan, Canada, had a Whistling Swan mate.

Although most out-of-range sightings have been of Whistling Swans in east Asia or of Bewick's x Whistling Swan intergrades along the Pacific flyways, a swan with yellow patches small enough to suggest that it was a Whistling Swan was spotted among the Bewick's Swans at Slimbridge in the 1968–69 and 1969–70 winters (the same bird) and a second individual in 1975–76. A swan named 'Serbia' that also had very little yellow on the bill, a possible Whistling x Bewick's Swan hybrid, visited Slimbridge in both 1996–97 and 1997–98, but there have been no other sightings of possible Whistling Swans at Slimbridge in recent years. For sites elsewhere in Britain, the British Birds Rarities Committee confirmed that an adult Whistling Swan was present at Nocton Fen, Lincolnshire, on 22 January 1998 (Rogers & the Rarities Committee 1999). The Committee describes the bird as 'only the second British Whistling Swan, with previous occurrences from 1986 to 1990 in Hampshire and (mainly) Somerset referring to a returning individual'. Whistling Swans are very rare visitors to the Netherlands. The Dutch rarities committee (the Commissie Dwaalgasten Nederlandse Avifauna), which has considered reports of rare birds in the Netherlands annually since 1979, and historical records dating back to 1924, has accepted fewer than 10 sightings of Whistling Swans in the country (van den Berg & Bosman 1999; van der Vliet *et al.* 2002). Most recently, a reported Whistling Swan in the area south of Den Oever (Noord-Holland), probably the same bird seen in northeast Holland earlier in the 2003–04 winter, turned out to be an aberrant Bewick's Swan. There have been five records to date of Whistling Swans in Ireland, and each record is believed (based on bill pattern) to refer to different individuals. Additionally, three of these five birds are thought to have returned to the same place in more than one winter. The most recent record was of a bird on the North Slob, Co. Wexford, in December 1990 that returned in March 1991 and December 1991 (O'Sullivan & Smiddy 1991, 1992; Irish Rare Birds Committee 1998; P. Smiddy pers. comm.). The first and second records of Whistling Swans in Estonia were of birds at Haeska, Martna, in November 1990 and April 1995 (Davies 2001).

The occasional records of interbreeding in the wild help to reinforce the case for conspecificity of Bewick's and Whistling Swans (Evans & Sladen 1980). The closer proximity of Whistling Swans in North America to the far eastern Bewick's Swan population means that mixing of the two populations is more likely to occur across the Bering Straits than across the Atlantic Ocean. This and an increase in the number of Whistling Swans nesting in east Russia since the 1970s (Chapter 2) probably accounts for the higher frequency of Bewick's and intergrade sightings in North America, and of Whistling Swans in Russia and Japan, than of Whistling Swans in northwest Europe. Despite the much more extensive overlap of the ranges of Bewick's and Whooper Swans, there are still no definite cases of Bewick's and Whooper Swans interbreeding in the wild, although it has been known in captivity. Since there are records of Whooper Swans breeding with Mute Swans in the wild, it seems likely that Bewick's x Whooper Swan pairings may occasionally

occur. The remoteness of the swans' main breeding grounds in the Russian Arctic would reduce the likelihood of a mixed pair being observed during the summer, but it is perhaps surprising that Bewick's \times Whooper Swan pairs are not occasionally reported in the winter months. Any hybrid offspring also would again be difficult to recognise, because of the similarity in the Bewick's and Whooper Swans' morphology and bill markings.

1.1.4 *Genetics studies*

The classification of plants and animals tends to be a movable feast, because taxonomists are concerned not only with grouping similar organisms into the same category, but also with describing the proximity of species in evolutionary terms. Traditionally this was based on studies of morphology, physiology, plumage and behaviour (particularly courtship displays), sometimes linked with fossil evidence. All extinct swans for which there is fossil evidence are from the northern hemisphere, with the exception of *Cygnus sumnerensis* from New Zealand (Brodkorb 1964). The earliest swans now attributed to Cygnini are *Cygnus mariae* and *Paracygnus plattensis* from the late Miocene of North America (Bickart 1990; Callaghan *et al.* 2005). More recent developments in avian genetics have enabled us to determine similarities between species at a molecular level, and thus to deduce their relationships over time, but even the detailed molecular studies give varying results depending on the types of analyses undertaken (Callaghan *et al.* 2005). In particular, the evolutionary status of the Coscoroba Swan, and also whether Bewick's Swans and Whistling Swans are genetically discrete, have given rise to some debate. Certainly the hybridisation of Bewick's Swans and Whistling Swans in the wild, and the cline in their bill patterns, lent some preliminary support to the view that they should be treated as a single species.

A recent PhD study at Nottingham University on the population and evolutionary genetics of swans (Harvey 1999) indicated that the Coscoroba Swan forms a sister group to the swans and geese, together with the Cape Barren Goose *Cereopsis novaehollandiae*, to which it is most closely related. This study suggested that the Black-necked Swan is the most ancient of the swan species, followed by the Black Swan, the Mute Swan, then the northern swans grouped together. However, morphological studies (Livezey 1996) and molecular studies using longer sequences but fewer species than the Nottingham study (Harshman 1996) suggested a sister relationship between the Black-necked Swans and the Black Swans. Molecular studies of the commonly sequenced cytochrome *b* gene have confirmed the difficulties of resolving relationships between the four northern migratory swans. This is probably because the four lineages separated at about the same time, but there is agreement that these swans are more closely related to each other than to the other swan species (review in Callaghan *et al.* 2005). Although there is no reason to separate Bewick's Swans and Whistling Swans on the basis of sequence divergence amongst the eight swan species and subspecies, preliminary population level analyses (using mitochondrial D-loop sequencing) suggest that they are genetically distinct. This indicates that speciation is underway and may continue if the level of interbreeding remains low (Harvey 1999).

1.2 BEWICK'S SWANS IN AVICULTURE

Bewick's Swans have long been kept in captivity. These are usually injured birds incorporated into waterfowl collections in Europe, but swans from the eastern population have also been sent from China to America. A wounded male survived for many years

in Anjou during the latter half of the 19th century (Rogeron 1883). Blaauw (1904) described plumage changes in a young bird, winged on the Zuiderzee in the Netherlands, which was brought to him to keep. The Duke of Bedford reported that Bewick's Swans bred occasionally in captivity, the first record being one at Woburn, Bedfordshire, before 1914, but no dates or details were given (Delacour 1954). A hybrid between an eastern Bewick's Swan female and a male Whistling Swan was reared in Connecticut in 1942 (Delacour 1954). More generally, although most swan species regularly rear young in zoological gardens, breeding the Arctic-nesting Bewick's and Whistling Swans at lower latitudes has proved difficult. A wild male Bewick's Swan, thought to be in its second winter, was caught at Slimbridge in 1948 and was paired with a wild-caught adult female ('Mrs Noah') obtained from Holland in 1950. On 2 June 1956 they began nest building; two eggs hatched at the end of the month and one chick fledged (Johnstone 1957; Evans 1975). Thereafter the pair bred regularly until the death of the male in 1962. The female did not breed again for several years, but subsequently paired with one of her 1961 offspring to raise seven cygnets to fledging between 1966 and 1969 and, following his death in 1969, reared seven more cygnets when paired to one of her 1962 offspring from 1973 to 1982. The first report of Whistling Swans breeding in captivity was near Winnipeg, Canada, in 1945 (Delacour 1954). The species did not breed in Europe until 1976 when two cygnets were hatched and raised at the Flamingo Gardens and Zoological Park at Olney, Buckinghamshire. A pair of Whistling Swans at Slimbridge also bred successfully in the same year; two offspring were reared in 1976 and 10 from two clutches in 1977 (Evans 1977b; Kear 1977, 1978).

'Mrs Noah' remains by far the most successful breeding Bewick's Swan to have been kept in captivity. By the time of her death in 1982, aged at least 33 years, she had laid 165 eggs and reared 27 cygnets to fledging. Only 13 other Bewick's Swans have bred in Wildfowl & Wetlands Trust collections, of which nine were her offspring and two her grand-offspring. Other records of Bewick's Swans breeding in captivity are at Takamatsu, Japan, in 1962; at Moscow in several years since 1968; and at Askaniya-Nova, in the former USSR in 1971 (Evans 1975). The reason why Bewick's and Whistling Swans are more difficult to breed in captivity than other swan species may be linked with their breeding distribution in the wild. Photoperiod is thought to regulate the timing of the migratory and reproductive cycles (Murton & Westwood 1977; see Chapter 3) and the day-length even in mid-summer at most zoological gardens may be too short to stimulate laying in these High Arctic nesting species. Certainly captive Bewick's Swans breed late compared with other wildfowl at the Wildfowl & Wetlands Trust; some 15 hours of daylight appear to be necessary before they start to lay (Kear 1972; Murton & Kear 1973).

1.3 BEWICK'S SWANS: A CLOSER LOOK

1.3.1 *Sex and age differences*

Like other swan species, there is no major difference in physical appearance between male and female Bewick's Swans. Adult swans, aged two years or more, have white plumage, black legs and feet, and the highly variable black-and-yellow bill markings. Some individuals may have rusty stains on the head, neck and underparts if they have been frequenting iron-rich waters, but this usually wears off upon moving to a new site. The yellow markings on the bill are usually cadmium yellow in adults; paler shades may be

indicative of ill health, particularly if the yellow is blotchy. Less common is a strong orange coloration on the bill, sometimes in birds with normal bill colour in the preceding or subsequent winter (Evans 1977a). The reason for this is still unclear but may be due to changes in diet, since swans with orange or pale bills may return with a normal yellow bill colour in subsequent years. Similarly, although most Bewick's Swans have a dark brown iris, a small proportion has grey-blue eyes. Eye colour seems to be consistent from one year to the next.

Juveniles can be distinguished quite easily during their first winter by their grey plumage and grey-pink bill. The grey plumage becomes whiter as the winter progresses, but yearlings can usually be aged in their second winter by traces of grey juvenile feathering in the white adult plumage. Grey feathering is rarely seen in third-winter birds, although some third-summer birds retain grey feathers on the head and neck (J. Beekman pers. comm.; Rees *et al.* 1997a). Bill colour also develops during the first winter, darkening from the tip as the young birds lose their reddish-pink bill markings. The outline of the adult bill pattern, albeit ill-defined, appears in chalk white tinged with yellow by early spring. Most swans have developed their adult bill markings by one year of age, although pink patches may remain on the bill into the second winter. Except in leucistic birds (see p. 28), these have usually turned black by the third year. The stage of development reached by the young, in terms both of whitening of the plumage and definition of the bill pattern, varies between broods. This may be due to differences in age, to the quantity and quality of food at different sites and, perhaps, also to their ability to gain access to the food available. The calls of juveniles are also diagnostic in that first-winter birds make higher pitched wheezing calls, rather than the musical bugling of the adults.

Downy young Bewick's Swans are very similar to the newly hatched young of other swan species, and cannot readily be distinguished from Whistling Swans of the same age. The down is pale greyish-white in colour with slightly darker patterning on the head, neck and back, and lighter underparts. The bill is flesh pink, grey at the tip and along the sides. It is relatively smaller than that of Whooper Swan and Trumpeter Swan cygnets and with less down extending along from the base (Boyd 1972). Fledging occurs at 60–70 days, usually in mid- to late September in the wild (Chapter 5).

Although there is no difference in the plumages of the two sexes, male and female Bewick's Swans can often be separated in the field by differences in body size. This is easiest for paired birds, since the two members of a pair can be compared directly. The sex of each individual can also be determined by cloacal examination when the birds are caught for ringing. Measurements made of Bewick's Swans' wing length, skull length, bill length and tarsus length confirmed that males are generally larger than females in every age category (as adults, yearlings or cygnets). However, there was substantial overlap in the range of measurements recorded for the two sexes (Evans & Kear 1978; Rees *et al.* 1997a; Appendix 1). The number of instances where the female has proved to be larger than her mate is surprisingly low, although one female, misnamed 'Dougie', was not only bigger than her mate 'Estranita' but was also the more aggressive member of the pair. There is also a significant difference in the sizes recorded for each of the age categories, with yearlings being distinct from adults as well as from cygnets, but again there was some overlap in the sizes recorded across the age categories. Weight changes have been recorded only for the winter months, when they increase from a low level upon arrival at the wintering site in late October or early November to a maximum in late December or early January. The most rapid weight gain is in the first few weeks after

arrival (i.e. by mid-November). A decrease in body mass in late January and February, mirroring similar weight loss at this time recorded for other species of waterfowl, is followed by marked pre-migratory fattening in March, prior to departure on spring migration. Females have consistently higher abdominal profile scores (an indicator of body condition) than males throughout the winter, particularly if they have a mate, and this difference is most marked just before migration (Bowler 1994). The exception is single females, which are generally in poorer condition than single males, probably because they do not have a mate to protect them whilst feeding. Paired males have significantly lower abdominal profile scores than single males, indicating that protection of the female is achieved at the cost of reducing their own food intake. This is particularly evident for dominant males with mates and cygnets, which are in the poorest condition of all the social classes by March, whereas their cygnets showed a significant improvement in condition over the winter season (Bowler 1994, 1996).

1.3.2 Geographic variation

The extension of the Whistling Swan breeding range into east Russia, sightings of Bewick's Swan on the Pacific coast of North America, and reports of Bewick's \times Whistling Swan pairs suggest that there may be a gene flow between the western Whistling Swans and eastern Bewick's Swans, which could lead to geographic variation within the Bewick's Swan population. Bewick's Swans in the eastern part of the range are reputed to have larger bills than those further west (Boyd 1972), but the wide range in the measurements recorded for swans wintering in northwest Europe and the lack of biometric data available for swans in China and Japan means that there is currently no evidence of an increase in body size towards the eastern end of the range. There is strong evidence for a clinal variation across the Arctic in the amount of yellow on the Bewick's Swans' bills, however, with those in the east having a smaller proportion of yellow than those in the west. A comparison of the bill markings of Bewick's Swans showed that the proportion of black-neb bill patterns was higher at five sites on Honshu, the main island of Japan, than it was amongst those wintering in Britain. The proportion of yellownebs was correspondingly lower at the Honshu sites (Scott 1981; Table 1.1). Interestingly, while there was no difference in the bill pattern categories recorded at Slimbridge and Welney, there was a marked difference in the proportions of bill pattern types between different sites in Japan, which may perhaps be attributable to a combination of site fidelity and heritability of bill patterns from one generation to the next. Studies have shown that individual Bewick's Swans, accompanied by their mates and cygnets, return to the same wintering grounds in successive years, and that the offspring frequently continue using the site when they reach adulthood (Scott 1966). The presence of one or two particularly successful breeding pairs, therefore, may result in a high proportion of related birds being present

Table 1.1 Proportion of different bill pattern types in Bewick's Swan flocks in Japan and England. From Scott 1981.

Site	Number of birds checked	% Blackneb bill pattern	% Pennyface bill pattern	% Yellowneb bill pattern
Slimbridge	2,400	17.9	19.1	63.0
Welney	300	18.0	18.0	64.0
Japan	312	35.9	13.1	51.0

in the wintering flock. In contrast to Bewick's Swans, Whooper Swans in the eastern part of the range have yellower bill markings than those in the west (Brazil 1981), indicating that there is no parallel gene flow between the eastern Whooper Swan population and the Trumpeter Swans of North America.

1.3.3 *Leucistic Bewick's Swans*

During the 19th century Swinhoe (1870) described *Cygnus davidi*, an unusual specimen seen in a Peking museum. The mystery deepened since the specimen was lost and no other records reached the west, making it difficult to confirm its identity. The Peking swan was reported as being smaller than a Bewick's Swan with all-white plumage, a vermilion bill tipped by a black nail, and orange-yellow legs and feet. The area between the bill and eye was feathered, leading some to suggest that it was a Coscoroba Swan, although there was no explanation of how it got from South America to China (Evans & Lebreton 1973). Meanwhile, Dorogostaiskiy (1913) received a specimen from the ornithological collection of the Irkutsk Museum of the Russian Imperial Geographical Society (Eastern Department) of an adult male swan killed by peasant Filipov on the River Irkutsk in 1902, which upon examination Dorogostaiskiy judged to be *Cygnus davidi*. The Irkutsk bird had most of the physical characteristics of the swan described by Swinhoe, particularly extensive 'yellow' (rather than vermilion) markings on the bill except for a black nail, a feathered cere, all-white plumage, and brown-orange (not black) legs and feet. The measurements were again smaller than for an adult Bewick's Swan. Janet Kear (1972) pointed out that the degree of feathering described by Swinhoe, which was also noted for the Irkutsk specimen, is found in juvenile Bewick's Swans, that the size would be about right for a subadult bird, and that *Cygnus davidi* therefore might be a leucistic variety of *Cygnus columbianus bewickii*.

Leucism (from the Greek *leukos*, meaning 'white, bright, light', or in this case 'lack of colour') denotes pigment deficiency, which in turn is thought to be genetically determined. Leucism is well known in the Mute Swan, where the white phase, pale-footed individuals are also known as 'Polish Swans', following the import of these birds from the Baltic. A sexual imbalance of 'Polish Swans' on Rhode Island (10% of males and 26% of females) led to a genetic study that showed that colour inheritance is sex-linked in Mute Swans (Munro *et al.* 1968). A leucistic Bewick's Swan, named 'Needham', seen at Welney in the 1971–72 winter and at Slimbridge in 1972–73, was accompanied at Slimbridge by a normal mate and a completely white cygnet with flesh/chalk-grey legs.

Birds have also been reported with yellow legs (Hanby 1986), orange legs (Merne & Walsh 1991) and pink-red legs (Ogilvie 1986), with or without a predominantly pink bill. It is possible that leg colour changes over time, perhaps the bill darkens, or alternatively the different combinations may reflect different genetic coding (Evans & Lebreton 1973), but since these individuals are seen for only one or two years, it has not been possible to monitor changes over time or from one generation to the next. Bewick's Swans with yellow legs and normal bill colour seem to be the most common variant; they are noted in flocks in the Netherlands in most winters, and there is some evidence for this being an inherited characteristic. In a flock of 821 swans in the Wieringermeerpolder, Netherlands, in December 2001, there were eight yellow-legged birds, which appeared to be related. They were close together in the flock and one adult (with a blacknebbill pattern) was accompanied by a yellow-legged yearling (a pennyface) and at least one cygnet also with yellow legs (W. Tijssen and H. Schobben pers. comm.).

1.3.4 Bill pattern variation

Studies of individual animals are greatly facilitated if they can be identified by natural characteristics, particularly since it is often difficult to catch and mark all the animals artificially and undue stress can be caused in the process. The ability of trained observers to recognise individual Bewick's Swans by the variations in the swans' black-and-yellow bill markings, and thus identify every individual in the flock, is one of the main strengths of the Bewick's Swan study at Slimbridge. Differences in Bewick's Swan bill patterns were first recorded by Clem Acland in 1923. The artist Charles Tunnicliffe was clearly aware of this since he sketched Bewick's Swans with different bill patterns in the 1940s (see Tunnicliffe 1979). G  roudet (1962, 1963) and Sermet (1963) made similar observations in Switzerland, despite that country not being a major wintering haunt for the birds. Sir Peter Scott, watching the Bewick's Swans using the lake in front of his studio window, also noticed the bill-pattern variations, particularly in the intricate patterns over the culmen and behind the nares, and realised that the presence or absence of particular swans on the lake could be monitored from day to day. Moreover, Sir Peter noted that of the 24 birds identified in the winter of 1963–64, 16 returned the following winter, indicating that this method could be used to track individual swans over several years. He quickly appreciated the value of this technique for a detailed study of the species and the Slimbridge Bewick's Swan study commenced (Scott 1966). The more extended black-to-yellow interface on the Whooper Swans' bill markings, although also variable, is less pronounced than in Bewick's Swans, making it more difficult to differentiate between individuals in the field (Brazil 1981).

From the outset, the bill patterns of adult and yearling swans wintering at Slimbridge were drawn to facilitate subsequent recognition. Initially, Sir Peter, his wife Philippa and daughter Dafila Scott drew the bill patterns, and in due course other scientists were also involved in the study. The three main categories of yellowneb, blackneb and pennyface bill patterns (Section 1.1.3) were soon identified. Within each category there are numerous variations, ranging from broad differences in patterning on the forehead, in the shape of the yellow protrusion towards the nostril (known as the 'tooth'), in the lower forward quadrant on the side of the bill and at the gape. More subtle nicks and knobs at the black-yellow interface, or spots and mush (of yellow on black or black on yellow) are also useful at close quarters. With other cues such as under-bill colouring and pattern, eye and eyelid colour, body size, head shape, bill profile and behaviour (including frequenting a particular part of the swan lake at Slimbridge) also available to the observer, the level of variation is such that the swans seem more different over time rather than less so. At the start of the winter, when memory is a little rusty and swans are arriving en masse, the presence of the same mate helps to recall the identity of a pair, although of course this is not to be relied on because Bewick's Swans do re-pair following the death of a mate. A 'face book' is compiled for swans seen at Slimbridge each winter, which includes not only the drawings of their bills but also their names and associations, and this is also very useful for confirming who's who in subsequent years.

As the number of swans identified increased (the bill patterns of some 7,600 adults and second-winter birds have been recorded in the 40 years between 1963–64 and 2003–04), more systematic methods for recording and retrieving the swans' bill patterns were developed so that individuals could be recalled in subsequent years without relying totally on human memory and the face book (Rees 1981 gives a review). Many of the patterns proved to be asymmetrical, which helped to tell birds apart but made it more difficult to develop a

system for filing the bill patterns of different swans. Pennycuik (1978) demonstrated that only 29% of swans have sufficient information in their markings on the right side alone for accurate identification. Nevertheless, a code was developed to describe the whole bill pattern in numerical terms, which could then be stored on computer. Now when an unknown swan arrives, its bill pattern code can be typed into the computer and compared with the codes of swans already incorporated on the database. The computer then lists the swans that approximate most closely to the new bird (Rees 1981). The coding and computerisation of Bewick's Swan bill patterns was used during the 1980s since it proved effective in retrieving the identity of swans not immediately recognised, but it remains a time-consuming system. Only a small number of birds were found to have been missed each winter (one or two birds not identified), so identification by computer has been temporarily dropped, pending the development of a less labour-intensive process. The mushy grey-pink bill patterns of cygnets are too ill-defined for identification purposes even within a winter season, although broad likenesses may be noted between members of the same brood. Cygnet bill patterns therefore are not recorded, but their identity in subsequent years can be determined by ringing and through association with their parents on returning as yearlings.

The accuracy of the bill-pattern recognition system has been tested and proven on several occasions. For instance, when experienced swan watcher Dafila Scott was asked to identify swans from slides taken two weeks earlier she correctly named the birds in 29 out of 30 good quality slides and 23 out of 30 of those less clearly portrayed (Bateson 1977). Recognition tests have also shown that swans can be identified reliably over a period of years; a comparison of photographs showed that although small changes in bill pattern may occur, usually in the upper part of the culmen, observers familiar with Bewick's Swans were able to identify the birds without difficulty, and even inexperienced observers could tell the birds apart (Evans 1977a). The greatest changes in bill patterns (excepting cygnets) occur between the second and third winters, but birds first identified as yearlings can usually be recognised upon returning as adults. One factor that helps immensely for observers learning to identify swans for the first time is that the birds arrive in stages during the autumn. It is therefore possible to draw and become familiar with a relatively small number of individuals when they first arrive, so that these are instantly recognisable by the time the next birds appear at the wintering site.

1.3.5 Heritability of bill patterns

Since the faces of individual Bewick's Swans are highly distinctive, it might be expected that offspring would inherit their bill pattern from their parents. Moreover, since humans are able to identify individual swans at a glance, it is possible that the birds also identify each other (particularly their mates and offspring) by sight. Certainly, paired birds that become separated during migration and spend the winter in different parts of Europe usually return together the following year if both individuals survive. This is not solely due to them returning to the same breeding territory. Members of a pair that arrive separately at a wintering site, sometimes weeks apart, recognise each other almost at once and reunite in a flock of more than 300 birds. Also, it is not unusual for a swan to peck at a bird feeding with its head under water only to discover, when the startled bird looks up, that it has pecked its own mate. On these occasions the pair may greet each other with head bobs or courtship displays, usually without vocalising, and then resume feeding side by side. Yet although Bewick's Swans have variable bill patterns that can be used to distinguish between individuals, it is unlikely that this feature is of crucial importance for recognising a mate