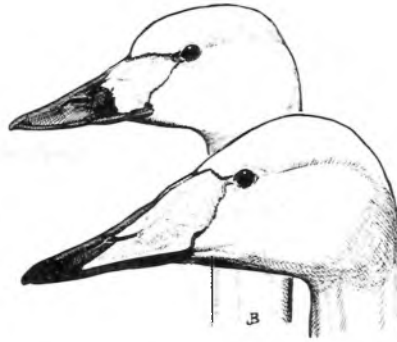


The Third International Swan Symposium: A Synthesis

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Introduction

The Third International Swan Symposium, serving as the main outlet for swan research since the Second Symposium in 1981, provided data from 14 countries on all species of swans. The goal of this review is to integrate the main issues addressed at the Symposium and to attempt a preliminary, but far from thorough, synthesis with previous work on swans and other species. Most references are to articles published in this Proceedings (referenced with the authors last name only; 'a' and 'b' indicate order of appearance in this Proceedings) and papers or posters presented at the Symposium but published elsewhere.

Distribution and status

In the last 20 years, most species of swans have increased in numbers, and many have expanded their range. Factors which are believed to have contributed to population growth in various areas include effective habitat protection, the control of hunting, increased food availability in the form of agricultural crops, and increased availability of ice-free waters in industrial areas.

Population increase and range expansion

Mute Swan populations throughout Europe and the Eastern Baltic area have increased approximately 30% since the 1970's (reviewed in Wieloch, see also Kuresoo). In the Central Palearctic, the Mute Swan population has spread north and east into its former breeding range and has increased nearly three-fold since 1978 (Krivonosov a). It is concentrated in the Black Sea area (Ardamatskaya & Korzyukov), the Volga River delta of the Caspian Sea (Krivonosov b), and the Kazakhstan area (Wieloch, Vinogradov & Auezov, Krivonosov a).

Mute Swans of the Scandinavian-Baltic and Central-European groups have expanded their range towards the south and east (Wieloch, Czapulak), establishing breeding populations in Yugoslavia, Hungary, and particularly in the Western Ukraine (Korzyukov *et al.*, Serebryakov *et al.*). In some areas breeding sites of European and Black Sea individuals are as close as 150 km and exchange between the two populations is becoming increasingly likely (Wieloch, Korzyukov *et al.*).

In North America, the Eastern and Western Populations of Tundra Swans, which are largely independent of one another (Limpert *et al.*), have increased since 1955 at an average annual rate of 2.4% and 1.8% respectively (Serie & Bartonek a). Similarly, Trumpeter Swans of the Alaska breeding population increased 8.4% per year from 1970 to 1985 (Anon. cited in McKelvey *et al.*, see also Conant *et al.*), and the Rocky Mountain Population has doubled since 1977 (Gale *et al.* 1987, Mitchell *et al.*).

There is little information on recent changes in numbers of breeding Bewick's and Whooper Swans in the U.S.S.R., although some local breeding populations are known to have experienced declines (Gorelov *et al.* 1987, Kalyakin 1987, Mineyev 1987, Perfiliev 1987, Vinokurov 1987, Kondratiev a) and others to have increased (Roslyakov 1987, see also Ravkin). In Finland, Whooper Swans have increased in numbers an average of 11% per year since 1950 and have expanded their range 25 km per year (Haapanen). The Icelandic population of Whooper Swans, which is primarily independent of the continental Eurasian population, is believed to be approximately stable at 14,000 (Gardarsson).

Although there are no data on changes in numbers of swans throughout South America, Black-necked Swans have responded well to protection in Chile. On Torca Lagune, the number of wintering swans has approximately tripled since protection began in 1982, and the number of breeding pairs has remained rela-

tively stable. On Rio Cruces, total numbers have doubled each year since protection began in 1985, and the number of breeding pairs has increased nearly three-fold (Schlatter *et al.* a).

No new information on the status of Black Swans in Australia and New Zealand was presented at the Symposium. In general, Black Swan populations are held in check with human intervention, and the breeding population on a given wetland fluctuates widely due to changes in water level and food availability (Williams 1981).

In summary, Mute, Tundra, and Trumpeter Swan populations are increasing; some local breeding populations of Whooper and Bewick's Swans are increasing and others decreasing; there is little information on the range-wide status of South American swans; and no recent information on Black Swans.

Variation in winter distribution

Swans and other waterfowl are known to respond to weather conditions by adjusting their winter distribution (Cramp & Simmons 1977). Mute Swans of the Scandinavian-Baltic group, some of which remain on their breeding grounds in the Eastern Baltic during mild winters (Kuresoo), are found in the Netherlands in large numbers during severe winters (Dirksen & Esselink). Mute Swans in other regions of Europe (Wieloch) and in the Caspian Sea area (Krivonosov b) also winter in more southern areas during severe winters. Remarkably, in some years cygnets in the Black and Caspian Sea areas appear to winter in different areas than their parents and the majority of other adults (Bacon pers. comm., based on flocks with 80-90% cygnets), although little is known of this phenomenon.

Winter severity also affects the distribution of the northern breeding swans. Only small numbers of Whooper Swans remain as far north as the Eastern Baltic (Kuresoo) during severe winters, and in Sweden they are restricted to small areas of open water where they depend on human provisioning (Mathiasson). Likewise, Tundra and Bewick's Swans change wintering locations (and habitat preferences) directly in response to food availability and winter severity (Munro 1981, Dirksen *et al.*).

In the southern hemisphere, where drought rather than ice leads to seasonal fluctuations in food availability, Black-necked Swans (Schlatter *et al.* a, Vaz-Ferreira & Rilla) and Black Swans (Braithwaite 1970) respond with nomadic movements among wetlands, some-

times over great distances.

Breeding biology and population dynamics

This section addresses variation in breeding success within populations, while the review of comparative demography (Bart *et al.* a) addresses variation in demographic parameters between populations and species.

Factors affecting probability of breeding, clutch size, and juvenile and adult survival

i) cold weather during winter

The most extensive data on the impact of severe weather are on Mute Swans and covers a wide range of climates and latitudes, including Denmark (Bacon & Andersen-Harild 1989; Andersen-Harild 1981a), the Netherlands (Beekman, Esselink & Beekman), England (Coleman *et al.*, Walter *et al.*, Perrins, Ogilvie 1967), the Volga River delta (Krivonosov b) and the Black Sea area (Ardamatskaya & Korzyukov). In each of these areas, Mute Swan young survived less well during cold winters than during mild winters. In most areas adult survival was probably also lower (e.g., Andersen-Harild 1981a; Coleman *et al.*).

Severe winters also affected reproduction during the following year. Adults were less likely to attempt breeding after cold winters (Bacon & Andersen-Harild 1989; Krivonosov b; Ardamatskaya & Korzyukov), and those that bred produced smaller clutches (Bacon & Andersen-Harild 1989, Krivonosov b, Beekman, Walter *et al.*, Czupalak & Wieloch). Since swans lose body condition during severe winters (e.g., Andersen-Harild 1981b) and body condition at the time of laying strongly influences reproductive success (Beekman, Walter *et al.*), a loss of body condition is probably the mechanism by which the previous winter's weather affects reproduction.

The effect of severe winters is less widely-documented for northern breeding swans. However, Trumpeter Swans have been shown to experience higher mortality during severe winters, particularly when water levels are low and thus subject to freezing (Gale *et al.* 1987). Also, Whooper Swans reproduce more successfully after mild winters (Nilsson 1979), and a similar process may be responsible for the large fluctuations in productivity seen in Bewick's Swans (Mineyev) and Tundra Swans (Serie & Bartonek a).

ii) the timing of spring, fall, and clutch initiation

The timing of spring thaw and fall freeze-over appear to be critical to arctic breeding swans because of the short time available to produce fledged young. Breeding pairs usually arrive first and leave last (Kondratiev b, Mineyev, Haapanen & Hautala). The importance of breeding season length is also suggested by evidence that northerly breeding populations of Whooper and Tundra Swans are less productive than southerly breeding ones (Haapanen, Bart *et al.* b), however the differences may instead be caused by differences in habitat quality or length of migration. Likewise, the lower clutch size and brood survival of Whooper Swans at highland vs. lowland breeding sites in Iceland was probably due to adverse weather which delayed nesting at the highland site, although habitat differences may also have had an effect (Rees *et al.*).

Late springs result in a loss of body condition, smaller clutches, and decreased probability of nesting successfully in arctic nesting geese which arrive on the breeding grounds with the nutrient reserves needed to breed (Ankney & MacInnes 1978, Barry 1962, Davies & Cooke 1983, Newton 1977, Prop *et al.* 1984). Arctic breeding swans probably also arrive with sufficient reserves, although we lack studies comparing available reserves to those needed for clutch production. There is direct evidence that late springs lead to decreased productivity in Tundra Swans (Lensink 1973, Dau 1981, McLaren & McLaren 1984). Also, the large variation in proportion of cygnets in wintering populations of Tundra and Bewick's Swans is believed to result, in part, from variation in spring thaw (Bart *et al.* b, Kondratiev, Mineyev, Serie & Bartonek a).

The timing of fall freeze-over is believed to be responsible for substantial mortality of Bewick's and Tundra Swan cygnets in some years (Kondratiev a, Mineyev 1987, and pers. obs.), however we lack direct evidence and estimates of the proportion dying. Arctic breeding geese and temperate breeding Mute Swans are also believed to suffer from early autumn freezes (Owen & Black 1989b, Kuresoo, Ardamatskaya & Korzyukov).

iii) body condition and date of clutch initiation

Mute Swan females increase body reserves on the breeding grounds and delay laying in order to do so (Beekman). The longer a female builds her body condition (up to a point), the larger

clutch she can produce. However, later clutches do not survive as well, and laying a large clutch decreases the female's subsequent body condition and survival rate (females in poor condition were near starvation during late incubation). A model of this process suggests that females in the typical weight range can optimize the number of young produced with a relatively early, smaller clutch which survives better, or with a relatively late, larger clutch which survives more poorly (Bacon & Beekman).

The outcome of similar models for northern breeding swans will be influenced by the degree to which females arrive on the breeding grounds with all the reserves needed for clutch production and the degree to which males help in incubation. Tundra and Bewick's Swans probably arrive on the breeding grounds with the needed reserves (see above), and they receive substantial help during incubation, while Whooper and Trumpeter Swans consume important nutrients after arrival (Ohtonen & Hautala) and males only rarely help with incubation. Studies of changes in body condition throughout the breeding season, similar to those on Mute Swans (see Beekman), would elucidate the breeding strategy of northern swans and the impact of loss of condition due to late springs or to severe weather during the previous winter.

iv) variation in food availability among years

The availability of food in a particular year is thought to affect the likelihood that young Lesser Snow Geese, *Anser caerulescens caerulescens*, will attempt to breed (Cooke & Rockwell 1988). This may be true of swans as well, particularly given the large annual variation in proportion of pairs attempting to breed (e.g., Kondratiev b).

Food availability during the breeding season is also known to affect clutch size and brood survival, and may have long-lasting effects on the reproductive success of young born during that year. During springs with low food availability resulting from low temperatures and high water, Trumpeter Swans laid smaller clutches (Gale *et al.* 1987). During years with favourable food availability, Mute Swan cygnets in the Netherlands reached the threshold weight at which fledging occurs at an earlier age (de Leeuw & Beekman), and probably had higher survival as a result (e.g., Bacon & Andersen-Harild 1989). Furthermore, the quality of the year of birth and thus the conditions under which one is raised, has been shown to have long-lasting effects on an individual's lifetime reproductive success in Mute Swans

(Bacon & Andersen-Harild 1989) and in several other avian species (reviewed in Newton 1989a).

v) territory quality

In Whooper Swans breeding in Finland, pairs nesting on food-poor territories laid smaller clutches than those on food-rich territories (Ohtonen & Hautala), and may have suffered higher brood mortality as a result of moving young broods to alternate feeding sites (Haapanen *et al.* 1973).

In Denmark, Mute Swans cygnets raised on territories with abundant vegetation had higher autumn weights than those raised on poor territories, and heavier young survived the winter better (Andersen-Harild 1981b). In England, Mute Swans cygnets raised on territories with abundant aquatic vegetation were allowed to remain on the territory longer and were thus protected from foraging competition with conspecifics (Scott 1984). A shortage of vegetation may also be the reason that Mute Swans nesting along estuaries in Ireland were less productive than pairs nesting in other habitats (Collins).

Territory quality may affect the degree of stress experienced by adults which remain on their territories to moult. Low food availability is thought to be responsible for the low weights found in some flocks of moulting Mute Swans (Andersen-Harild 1981b), and low weight is also known to delay the initiation of moult in adults (van Dijk & van Eerden).

Human disturbance may also affect productivity. For example, Mute Swans in Ireland and Staffordshire, England which nested in proximity to human activity suffered lower breeding success due to egg stealing (Coleman *et al.*, Collins, and references therein). Other potential disadvantages of nesting near human habitation include mortality due to lead poisoning (e.g., Sears & Hunt, O'Halloran *et al.*) and collisions with power lines (e.g., Coleman *et al.*, Collins, Ogilvie 1967).

vi) coloniality

Natural colonies of Mute Swans have recently formed in Denmark, Sweden, West Germany, East Germany, and the Volga River delta (reviewed in Wieloch). In Denmark, birds attempting to breed in colonies were only 25% as successful as those attempting to breed on territories (Bacon & Andersen-Harild 1989). The lower success of colonial breeders was due mostly to egg breakage during fights over nest-

ing sites (Bacon & Andersen-Harild 1987). Interestingly, in the very old, human-maintained colonies in England, aggression over nest sites is rare (Perrins & Ogilvie 1981), although newly hatched cygnets are sometimes drowned by aggressive adults (Fair 1985).

In Black Swans there is suggestive evidence that fledging success is higher on territories where offspring are raised in family groups, than in colonies where the majority of offspring are raised in creches (Williams 1981). In a large captive colony, Black Swans experienced both egg-breakage due to fights over nest sites and mortality of cygnets due to aggression (Braithwaite 1981).

Colonially nesting Black-necked Swans in Chile sometimes exhibit substantial aggression towards cygnets (Schlatter *et al.* b). The level of chick mortality varied with breeding density on three wetlands, from 83% mortality with 0.49 prs/ha, to 12% mortality with 0.07 prs/ha, to only 8% mortality with 0.02 prs/ha., suggesting that aggression and mortality may reflect the degree of competition over food. Our understanding of the reproductive consequences of coloniality would be greatly increased by systematic study of aggression within colonies and its relationship to the availability of nesting material, nest sites, and food in Mute, Black, and Black-necked Swans.

Even though colonial breeding is less successful than breeding on a territory, colonial breeding is better than not breeding at all. Coloniality in swans is believed to result when territories are not economically defensible (*sensu* Brown 1964) due to limited nest sites, locally abundant food (Bacon & Andersen-Harild 1987), or a food supply that is spatially and temporally unpredictable (Bacon & Andersen-Harild 1987, Kear 1972, Williams 1981, Braithwaite 1981). All three ecological conditions have been associated with facultative coloniality in other avian species as well (reviewed in Lott 1984). Coloniality in Mute, Black, and Black-necked Swans may have arisen independently as a result of analogous selective forces such as those mentioned above, but it may also, in part, reflect their common ancestry. A comparison between colonial and territorial systems would elucidate the ecological and social factors favouring each system.

vii) genetics

Mute Swans with different alleles at the lactate dehydrogenase locus have been shown to differ in their tendency to nest in colonies, and to differ in their breeding success within colonies

(Bacon & Andersen-Harild 1987, Bacon & Perrins). Similarly, territorial breeders with different alleles at the esterase locus have been shown to differ in clutch size (Birkhead *et al.* 1983) and fledging success (Walter *et al.*). The mechanism by which this difference is achieved is not known, although a difference in habitat preference is suspected (e.g., Bacon 1981). And finally, there is evidence that Polish morph Mute Swans have lower breeding success as adults and lower survival as juveniles (reviewed in Wieloch & Czapulak), possibly resulting in part from the tendency for adult males to reject Polish young (Norman 1977).

viii) age, breeding experience and length of the pair bond

In long-lived species, reproductive performance often increases with age during early life (e.g., Cooke & Rockwell 1988, Newton 1989b, Ollason & Dunnet 1988), and decreases with loss of a mate (Ollason & Dunnet 1988, Coulson & Thomas 1985, Owen & Black 1989b). In Bewick's Swans, breeding success increased with age and with duration of the pair bond irrespective of age (Scott 1988).

Although many studies are not able to separate the effects of age and breeding experience, there is evidence that these two factors influence breeding success in Mute Swans. In the Oxford area of England, the number of years since a female had first bred was an important determinant of clutch initiation date which in turn affected the number of fledged young produced (Walter *et al.*). In Staffordshire, England, established pairs were more likely to lay eggs than were newly established pairs (Coleman *et al.*). Established pairs were also more successful in Denmark, but breeding success did not increase with age or duration of the pair bond over the course of an individual's life (Bacon & Andersen-Harild 1989).

ix) body size, dominance, and post-fledging parental care

The body size of a male Bewick's Swan was shown to be an important determinant of both his and his mate's lifetime reproductive success (Scott 1988). The male's body size is known to affect his and his family's dominance status during winter (Scott 1980), but the importance of body size and dominance on the breeding grounds have not been studied. Surprisingly, body size was not correlated with lifetime reproductive success in Mute Swans in Denmark (Bacon &

Andersen-Harild 1989), even though males are known to fight vigorously over territories (Ogilvie 1967) and over nest sites in colonies (Bacon & Andersen-Harild 1987).

Post-fledging parental care in Bewick's and Tundra Swans serves to protect their offspring from foraging competition with adults in wintering flocks (Scott 1980, Earnst & Bart). Breeding ground studies of known-parentage offspring are needed to identify any long-lasting benefits of this protection and to explore the possibility of additional aid on the breeding grounds. Mute Swans also protect their offspring from foraging competition with flocked adults; some pairs allowed offspring to remain on their natal territory well after fledging (Scott 1984). Recently, Bacon & Andersen-Harild (1989) found that offspring raised on territories were able to breed either colonially or territorially, but offspring raised in colonies never succeeded in breeding territorially. This finding raises interesting possibilities for studies of how parental care or other experiences during early life affect subsequent reproductive success.

Foraging ecology

Swans are ideal subjects for investigating individual foraging strategies in relation to such variables as food availability, energetic needs, age, and social status.

In Tundra, Bewick's, and Whooper Swans, families and non-families differed in habitat use (Bart *et al.* b, Dirksen *et al.*; and Black *et al.*), and in some cases differed in feeding intensities (e.g., Rees & Bowler). Such differences, as well as the tendency to feed more intensively on spring staging grounds than during mid-winter (Rees & Bowler), are probably related to differences in energetic needs (Rees & Bowler, McLandress & Raveling 1981, Bortner, 1985).

The foraging ecology of Bewick's Swans feeding on tubers of *Potamogeton pectinatus* in the Netherlands has been studied in detail. Bewick's Swans preferentially selected large-sized tubers within patches, and there appeared to be a threshold density of tubers below which a patch was considered too unprofitable to exploit (Beekman *et al.*). When all patches were depleted below threshold densities, swans switched to alternate food sources (Dirksen *et al.*). Given the wide use of *Potamogeton* and other tubers by swans (e.g., Earnst & Bart, Kondratiev b, Schneider-Jacoby *et al.*, Owen & Kear 1972), these studies are likely to have

broad applicability in explaining foraging strategies and habitat use.

Conservation and management

Many successes in management and conservation were reported at the Symposium. The preservation of wetlands and the control of hunting has led to growth of swan populations in several areas (e.g., South America, USSR). The severe lead poisoning problem in England has improved since the ban on lead fishing weights (Sears & Hunt), although lead poisoning is still a problem in England and elsewhere (Sears & Hunt, O'Halloran *et al.*, Degernes & Frank). The hunting of Eastern Population Tundra Swans in North America has not yet had the desired effect of reducing the population size (Serie & Bartonek b), however, more years of data are needed to ascertain the success of this controversial (e.g. Sladen) management plan.

Symposium participants presented a variety of techniques for the study and management of swans. Recently developed techniques of treating lead poisoning (Degernes), of transplanting populations into more suitable habitats (Shea *et al.*), of determining age-specific survival rates of banded birds (Allen *et al.*, Bart), and of determining genetic relatedness (Meng & Parkin) have been used with success. Several authors suggested ways that survey techniques could be improved, such as standardizing meth-

ods among years and areas within a population's range (Conant *et al.*), flying transects that allow the reliability of the population estimate to be calculated (Serie & Bartonek a, Conroy *et al.* 1988), and taking account of differences in habitat use by families and non-families when estimating age-ratios (Bart *et al.* b, Sladen, Dirksen *et al.*, Black *et al.*). Such standardization, when combined with innovative aerial and satellite mapping technology (Conant *et al.*), promises to make future swan surveys more accurate and reliable.

The future

During the Symposium swan biologists from throughout the world expressed an eagerness to exchange ideas and to form collaborative projects. Such collaboration will make swans one of the few avian taxa that can be studied across the entire breeding range of each of its species. Likewise, the migratory swans will be among the only long-distance migrants that can be studied throughout their annual cycle, despite a migration that takes them across the borders of nations. Not only will this approach produce detailed information on each population, it will also lead to fruitful comparisons among species and among populations within species. As a result of such studies, swan biologists will be well-equipped to address important issues in conservation, population biology, and ecology.

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References

- Andersen-Harild, P. 1981a. Population dynamics of *Cygnus olor* in Denmark. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980, pp. 176-191. IWRB, Slimbridge.
- Andersen-Harild, P. 1981b. Weight changes in *Cygnus olor*. In: G. V. T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980, pp. 359-378. IWRB, Slimbridge.
- Ankney, C.D. & MacInnes, C.D. 1978. Nutrient reserves and reproductive performance of female Lesser Snow Geese. *Auk* 95:459-471.
- Bacon, P.J. 1981. Population genetics of *Cygnus olor*. In: G. V. T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980, pp. 389-394. IWRB, Slimbridge.
- Bacon, P.J. & Andersen-Harild, P. 1987. Colonial breeding in Mute Swans (*Cygnus olor*) associated with an allozyme of lactate dehydrogenase. *Biol. J. Linn. Soc.* 30:193-228.
- Bacon, P.J. & Andersen-Harild, P. 1989. Mute Swan. In: *Lifetime reproduction in birds* (Ed. I. Newton), pp. 361-386. Academic Press, London.
- Barry, T.W. 1962. Effects of late seasons on Atlantic Brant reproduction. *J. Wildl. Manage.* 26:19-26.
- Birkhead, M. Bacon, P.J. & Walter, P. 1983. Factors affecting the breeding success of the Mute Swan *Cygnus olor*. *J. Anim. Ecology* 52:727-741.

- Bortner, J.B. 1985. Bioenergetics of wintering Tundra Swans in the Mattamuskeet Region of North Carolina. Univ. of Maryland, M.S. Thesis. 64 pp.
- Braithwaite, 1970. The Black Swan. *Austr. Nat. Hist.*, Sept., 375-379.
- Braithwaite, 1981. Ecological studies of the Black Swan III. Behaviour and social organization. *Aust. Wildl. Res.*, 8: 135-146.
- Brown, J.L. 1964. The evolution of diversity in avian territorial systems. *Wilson Bull.* 76:160-169.
- Conroy, J.L. Goldsberry, J.R. Hines, J.E. & Stotts, D.B. 1988. Evaluation of aerial transect surveys for wintering American black ducks. *J. Wildl. Manage.* 52:694-703.
- Cooke, F. & Rockwell, R.F. 1988. Reproductive success in a Lesser Snow Goose population. In: *Reproductive success* (Ed. T.H. Clutton-Brock), pp. 237-250. University Press, Chicago.
- Coulson, J.C. & Thomas, C. 1985. Differences in the breeding performance of individual Kittiwake Gulls, *Rissa tridactyla* (L.). In: *Behavioural Ecology* (Ed. R.M. Sibly & R.H. Smith), pp. 489-503. Blackwell Scientific Publ., Oxford.
- Cramp, S. & Simmons, K.E.L. 1977. *Handbook of the birds of Europe, the Middle East, and North Africa: the birds of the Western Palearctic*. Vol. 1: Ostrich-Ducks. Oxford Univ. Press, Oxford.
- Dau, C. 1981. Population structure and productivity of *Cygnus columbianus columbianus* on the Yukon Delta, Alaska. In: G. V. T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980, pp. 161-169. IWRB, Slimbridge.
- Davies, J.C. & Cooke, F. 1983. Annual nesting productivity in Snow Geese: Prairie droughts and arctic springs. *J. Wildl. Manage.* 47:291-296.
- Fair, J. 1985. *The Mute Swan*. Gavin Press, Limington, U.K.
- Gale, R.S., Scott, J.M., Carpenter, J.W., and Reed, C. 1987. The history, ecology, and management of the Rocky Mountain Population of Trumpeter Swans. Unpubl. ms. 314 pp.
- Gorelov, M.S. Gorshkov, Y.A. Yemelin, G.A. Prokhorov, Y.V. 1987. Breeding of swans in Kuibyshev Oblast. In: *Ecology and migration of swans in the U.S.S.R.* (Ed. Syroyochkovicki, Y.E. translated by J. Dunning), p. 153-154. IWRB, Slimbridge.
- Haapanen, A., Helminen M., & Suomalainen H.K., 1973. Population growth and breeding biology of the Whooper Swan, *Cygnus c. cygnus*, in Finland in 1950-1970. *Finnish Game Res.* 33:39-60.
- Kalyakin, V.N. 1987. Swans of the northwestern Yugor Peninsula and Vaigach Island. In: *Ecology and migration of swans in the U.S.S.R.* (Ed. Y.E. Syroyochkovicki; translated by J. Dunning), pp. 102-105. IWRB, Slimbridge.
- Kear, J. 1972. Reproduction and family life. In: *The Swans*. Scott, P. & The Wildfowl Trust, pp. 80-124. Michael Joseph, London.
- Lensink, C. 1973. Population structure and productivity of whistling swans on the Yukon delta, Alaska. *Wildfowl* 24:21-25.
- Lott, D.F. 1984. Intraspecific variation in the social systems of wild vertebrates. *Behaviour* 88:266-325.
- McLandress, M.R. & Raveling, D.B. 1981. Hyperphagia and social behavior of Canada Geese prior to spring migration. *Wilson Bull.* 93:310-324.
- McLaren, M.A., & McLaren P.L., 1984. Tundra swans in northeastern Keewatin District, N.W.T. *Wilson Bull.* 96:6-11.
- Mineyev, Y.N. 1987. Ecology, numbers and conservation of swans in the northeastern European part of the U.S.S.R. In: *Ecology and migration of swans in the U.S.S.R.* (Ed. Y.E. Syroyochkovicki; translated by J. Dunning), pp. 18-21. IWRB, Slimbridge.
- Munro, R.E. 1981. Field feeding by *Cygnus columbianus columbianus* in Maryland. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980, pp. 261-272. IWRB, Slimbridge.
- Newton, I. 1977. Timing and success of breeding in tundra nesting geese. In: *Evolutionary ecology* (Eds. B. Stonehouse, & C. Perrins.), pp. 113-126. Univ. Park Press, London.
- Newton, I. 1989a. Synthesis. In: *Lifetime reproduction in birds* (Ed. I. Newton), pp. 441-469. Academic Press, London.
- Newton, I. 1989b. Sparrowhawk. In: *Lifetime reproduction in birds* (Ed. I. Newton), pp. 279-296. Academic Press, London.
- Nilsson, L. 1979. Variation in the production of young of swans wintering in Sweden. *Wildfowl* 30: 129-134.
- Norman, D.O. 1977. A role for plumage colour in Mute Swan (*Cygnus olor*) parent offspring interaction. *Behaviour* 42:314-321.
- Ogilvie, M.A. 1967. Population changes and mortality of the Mute Swan in Britain. *Wildfowl* 18:64-73.

- Ollason, J.C. & Dunnet, G.M. 1988. Variation in breeding success in Fulmars. In: *Reproductive Success* (Ed. T.H. Clutton-Brock), pp. 263-278. Univ. Press, Chicago.
- Owen, M. & Black, J.M. 1989a. Factors affecting the survival of Barnacle Geese on migration from the breeding grounds. *J. Anim. Ecol.* 58:603-617.
- Owen, M. & Black, J.M. 1989b. Barnacle Goose. In: *Lifetime reproduction in birds* (Ed. I. Newton), pp. 349-362. Academic Press, London.
- Owen, M. & Kear, J. 1972. Food and feeding habits. In: *The Swans*. Scott, P. & The Wildfowl Trust, pp. 80-124. Michael Joseph, London.
- Perfilyev, V.I. 1987. *Cygnus cygnus* and *Cygnus bewickii* in northern Yakutia. In: *Ecology and migration of swans in the U.S.S.R.* (Ed. Y.E. Syroyochkovicki; translated by J. Dunning), p. 158-159. IWRB, Slimbridge.
- Perrins, C.M. & Ogilvie, M.A. 1981. A study of the Abbotsbury Mute Swans. *Wildfowl* 32:35-47.
- Prop, J. van Eerden M.R. & Drent R.H., 1984. Reproductive success of the Barnacle Goose *Branta leucopsis* in relation to food exploitation on the breeding grounds western Spitsbergen. *Norsk Polarinstitutt Skrifter* 181:87-117.
- Roslyakov, G.Y. 1987. Swans of the Lower Amur region and Shantar Islands. In: *Ecology and migration of swans in the U.S.S.R.* (Ed. Y.E. Syroyochkovicki; translated by J. Dunning), pp. 160-161. IWRB, Slimbridge.
- Scott, D.K. 1980. Functional aspects of prolonged parental care in Bewick's Swans. *Anim. Behav.* 28:938-952.
- Scott, D.K. 1984. Parent-offspring association in Mute Swans (*Cygnus olor*). *Z. Tierpsychol.* 64:74-86.
- Scott, D.K. 1988. Reproductive success in Bewick's Swans. In: *Reproductive Success* (Ed. T.H. Clutton-Brock), pp. 220-236. Univ. Press, Chicago.
- Vinokurov, A.A. 1987. *Cygnus bewickii* in the Tamyra. In: *Ecology and migration of swans in the U.S.S.R.* (Ed. Y.E. Syroyochkovicki; translated by J. Dunning), pp. 162-163. IWRB, Slimbridge.
- Williams, M. 1981. The demography of New Zealand's *Cygnus atratus* population. In: G.V.T. Matthews & M. Smart (Eds.) *Proc. 2nd Int. Swan Symp.*, Sapporo, 1980, pp. 147-161. IWRB, Slimbridge.

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