Whooper Swan *Cygnus cygnus* egg production in different nesting habitats in Finland

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A total of 112 Whooper Swan nests with eggs were examined in Finland. Of these 40 were on the fens (mobile pairs) and 72 on ponds or lakes with rich vegetation (sedentary pairs). The clutch size of sedentary pairs, 5.08, was statistically significantly higher than that of mobile pairs, 4.40, ($F = 10.231$, $P<0.01$). Also, the relationship between clutch size to egg volume seems to be different in the two habitats. There did not appear to be any difference between laying date in different habitats. Horsetails are typical in lakes and ponds and are of great value as the food of Whooper Swans. A possible reason for the higher clutch size of sedentary pairs may be the quality of the food eaten by the female during laying, especially the high protein content of growing horsetails.

Haapanen *et al.* (1977) have classified the nesting habitats of Whooper Swan *Cygnus cygnus* in Finland into two classes according to their breeding and feeding environment. In the first case, all habitat requirements are fulfilled within a restricted area. These nesting habitats are ponds and lakes providing enough food for the brood during the whole breeding period (sedentary pairs). In the second case, the Whooper Swans must use larger areas. The nests are on fens or lakes, where the food supply is not good enough for the brood during the whole summer. After hatching the brood must move to another site with rich vegetation. These can be fens, ponds, lakes or brooks (mobile pairs).

Haapanen *et al.* (1973a) discovered that brood size of the sedentary pairs in late July was significantly larger than that of the mobile pairs. The clutch size of the sedentary pairs examined was also larger than that of the mobile pairs, but the data were insufficient for detailed analysis. Haapanen *et al.* (1973a) suggested that the most probable reason for the difference in brood size was higher juvenile mortality for mobile pairs just after hatching. Hansen *et al.* (1971) have also pointed to the possibility of higher mortality among mobile pairs of Trumpeter Swans *C. buccinator* in Alaska.

The Whooper Swan population in Finland has grown rapidly in the last few decades (Haapanen 1987). This has given a better opportunity to examine egg production in different nesting habitats. In this study, the differences in clutch size between sedentary and mobile pairs in Finland are examined. The variation is discussed in respect to the availability of food and timing of nesting.

Table 1. The number of Whooper Swan clutches of different size in different nesting habitats in Finland. 1. 1988, 2. other years from 1960 to 1989 and clutches by Haapanen *et al.* (1973a) in years 1950-70. The significance of the difference between nest habitats (F and p, ANOVA) are indicated.

Nest habitat		Clutch size 2	3	4	5	6	7	*n*	Mean±SE	F	p
1.	Fens		4	3	6	1		14	4.29±0.27	6.822	<0.05
	Ponds			3	7	5		15	5.13±0.19		
2.	Fens	2	3	6	12	2	1	26	4.46±0.23	4.952	<0.05
	Ponds	1	4	10	24	11	7	57	5.07±0.15		
Total	Fens	2	7	9	18	3	1	40	4.40±0.17	10.231	<0.01
	Ponds	1	4	13	31	16	7	72	5.08±0.13		

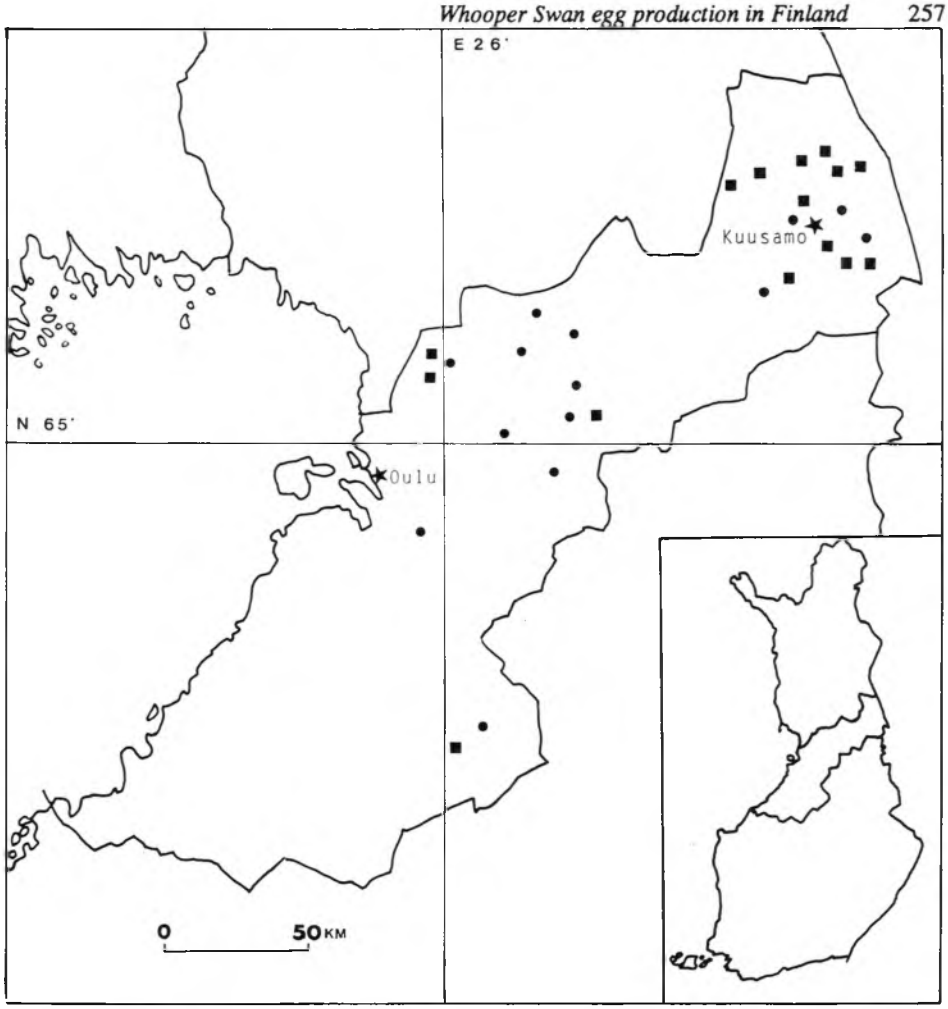

Figure 1. The whole study area in Finland and the nest of the sedentary (■) and the mobile (●) pairs of the Whooper Swans in summer 1988.

Materials and Methods

Since 1960, 91 Whooper Swan clutches have been examined by the authors in the northern part of Finland and a further 21 clutches have been examined by Haapanen (1973a) in years 1950-70. Thus a total of 112 nests were examined, of which 72 belonged to sedentary pairs on ponds and lakes with rich vegetation and 40 nests belonged to mobile pairs from fens (Table 1).

The most controlled data were collected during June 1988 when 29 nests with eggs or recently hatched young were checked, so that final clutch size was confirmed with certainty. Fifteen of these nests were of the sedentary pairs on the ponds or lakes and 14 of the mobile pairs on the fens (Fig. 1). Timing of the egg laying of 13 sedentary and nine mobile pairs was determined by floating the eggs. Egg size variation (length and width) was measured from 14 nests of sedentary pairs and nine nests of the mobile pairs in summer 1988 and one nest of both mobile and sedentary pairs in summer 1989. The volume index of the eggs was calculated as follows: (egg length) x (egg width)^2.

Results

When all data from 1950-89 were analysed, clutch size of the sedentary pairs was significantly higher than that of the mobile pairs ($\bar{x}$ = 4.40, vs. $\bar{x}$ = 5.08, respectively; F = 10.231, P<0.01). The same pattern was found when only the more controlled data from 1988 were

Table 2. The volume index of Whooper Swan eggs from different clutch sizes in different nesting habitats in Finland (n is the number of nests). The volume index is calculated as follows: (egg length cm) x (egg width cm)^2

Nest habitat	Clutch size 2 Mean SE	*n*	3 Mean SE	*n*	4 Mean SE	*n*	5 Mean SE	*n*	6 Mean SE	*n*	Total egg biomass per clutch Mean SE	*n*
Fens	638.4	(1)	640.6±31.45	(3)	623.2	(1)	600.3±27.93	(4)	546.1	(1)	613.1±16.14	(10)
Ponds					583.5±8.85	(3)	605.2±13.74	(7)	612.8±15.84	(5)	603.4± 8.47	(15)
Total	638.4	(1)	640.6±31.45	(3)	593.5±11.73	(4)	603.5±12.56	(11)	601.7±17.02	(6)	607.3± 8.07	(25)

used ($\bar{x}$ = 4.29 vs. $\bar{x}$ = 5.13, respectively; F = 6.822, P<0.05) (Table 1).

There was no difference in laying date between the two habitats as determined from nests where eggs were aged using the floating test.

There was no difference in the mean volume of eggs from different nesting habitats (Table 2). The relationship of egg volume to clutch size for pairs on the fens was negative and that of ponds positive (slopes ±0 S.E., -21.4 ±0 11.8 and 13.8 ±0 11.6, respectively). Although the slopes do not differ significantly from zero, they are significantly different from each other (t = 2.11, P<0.05).

Discussion

Hansen *et al.* (1971), Haapanen *et al.* (1973a) and Nilsson (1979) have proposed that weather conditions during the winter and spring preceding nesting affect brood production of the swans; the warmer the preceding winter and the earlier the spring, the better the fledging success. According to the present study, Whooper Swan egg production is also dependent on the habitat. The larger brood size observed for sedentary pairs, compared to mobile pairs after hatching (Haapanen *et al.* 1973a) will be due, at least in part, to the larger clutch size of sedentary pairs.

According to Lack (1967, 1968) clutch size of nidifugous birds like waterfowl, has evolved primarily in relation to the average availability of food for the laying female. Lack found an inverse relationship between egg size and clutch size among species of waterfowl. Proportionately larger eggs may be advantageous because the chicks which hatch from them have a greater chance of survival. However, larger eggs can evolve only at the expense of producing fewer eggs.

According to this hypothesis, it might be advantageous for mobile pairs of Whooper Swans to invest in the quality (as indicated by egg volume) of their eggs and so improve the survival of young during the critical post-hatching time. Sedentary pairs, however, might benefit from investing in brood size, because mortality during the days just after hatching on the ponds and lakes with rich vegetation may be lower than that recorded for mobile pairs on the fens.

Rohwer (1988) and Rohwer & Eisenhauer (1989), however, did not find any inverse relationship between egg size and clutch size in an inter- and intraspecific analysis of waterfowl. They thus believed that Lack's hypothesis concerning the relationships between clutch size and egg size needs further testing.

In this study, comparison of the slopes of regression lines of fen and pond nests showed that in poor food condition on the fens Whooper Swans might invest to the quality of eggs by increasing the size of eggs at the expense of the clutch size. This observation is in accordance with Lack's hypothesis. By contrast, in good food condition on the ponds the size of the eggs increases with the clutch size. However, the number of clutches examined was small and more measurements are needed for further analysis of relationship between clutch size and egg size of Whooper Swans nesting in different habitats.

Eldridge & Krapu (1988) reported that Mallard *Anas platyrhynchos*, fed on an enriched diet (especially protein) before laying produced larger clutches and larger eggs than Mallard fed on wheat. Similarly, the provision of food rich in protein prior to laying led to an increase in the size of the clutch and eggs of Magpies *Pica pica* (Högsted 1981). Haapanen (1982) found exceptionally high clutch sizes for Whooper Swans which were fed by people living near their nestlake, indicating in a similar manner that food may have a direct effect on the laying female.

On the lakes with rich vegetation, horsetails *Equisetum fluviatile* are typical and are of great value as the food of Whooper Swans (Haapanen *et al.* 1977). Thomas & Prevett (1982) have shown that horsetails grow quite early in the spring and the young plants in particular have a

good protein content. The food on nesting sites of sedentary pairs before laying might thus be of better quality than that experienced by mobile pairs and this might influence the egg production of females.

Clutch size of many waterfowl is known to be smaller in late nests (Klomp 1970, Winkler & Walters 1983, Rohwer & Eisenhauer 1989). The clutch size of the Finnish Whooper Swans was also smaller in the late nests than in the earlier ones (Haapanen *et al.* 1973b). In the present study, however, during summer 1988 there were no differences in the timing of nesting between the sedentary and mobile pairs. Thus the difference in clutch size between nesting habitats may not be connected to the timing of laying.

Egg production of young birds of many species has been shown to be lower than that of older birds (Klomp 1970). However, data is not available to examine this possibility further.

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References

Eldridge, J.L. & Krapu, G.L. 1988. The influence of the diet quality on clutch size and laying pattern in Mallards. *Auk* 105:102-110.

Haapanen, A. 1982. The life history of a female Whooper Swan *Cygnus cygnus*. *Ornis Fennica* 59:153-154.

Haapanen, A. 1987. Suomen laulujoutsenkanta. *Lintumies* 22:146-150. (In Finnish).

Haapanen, A., Helminen, M. & Suomalainen, H.K. 1973a. Population growth and breeding biology of the Whooper Swan, *Cygnus c. cygnus*, in Finland in 1950-1970. *Finnish Game Res.* 33:39-60.

Haapanen, A., Helminen, M. & Suomalainen, H.K. 1973b. The spring arrival and breeding phenology of the Whooper Swan, *Cygnus c. cygnus*, in Finland. *Finnish Game Res.* 33:31-38.

Haapanen, A., Helminen, M. & Suomalainen, H.K. 1977. The summer behaviour and habitat use of the Whooper Swan, *Cygnus c. cygnus*, in Finland. *Finnish Game Res.* 36:49-81.

Hansen, H.A., Shepherd, P.E.K., King, J.G. & Troyer, W.A. 1971. The Trumpeter Swan in Alaska. *Wildlife Monographs* 26:1-83.

Högsted, G. 1981. Effect of additional food on reproductive success in the Magpie (*Pica pica*). *J. Anim. Ecol.* 50:219-229.

Klomp, H. 1970. The determination of clutch size. A review. *Ardea* 98:1-124.

Lack, D. 1967. The significance of clutch-size in waterfowl. *Wildfowl Trust Ann. Rep.* 18: 125-128.

Lack, D. 1968. *Ecological adaptations for breeding in birds.* Methuen, London.

Nilsson, L. 1979. Variation in the production of young of swans wintering in Sweden. *Wildfowl* 30:129-134.

Rohwer, F.C. 1988. Inter- and intraspecific relationships between egg size and clutch size in waterfowl. *Auk* 105:161-176.

Rohwer, F.C. & Eisenhauer, D.I. 1989. Egg mass and clutch size relationships in geese, eiders and swans. *Ornis Scandinavica* 20:43-48.

Thomas, W.G. & Prevett, J.P. 1982. The role of horsetails (Equisetaceae) in the nutrition of northern breeding geese. *Oecologia* 53:359-363.

Winkler, D.W. & Walters, J.R. 1983. The determination of clutch size in precocial birds. *Curr. Ornithol.* 1:33-68.

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