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Comparative study of the breeding success of Whooper Swans *Cygnus cygnus* nesting in upland and lowland regions of Iceland

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The study assessed the reproductive success at different stages of the breeding season of Whooper Swans *Cygnus cygnus* from two geographically distinct areas of Iceland, one an upland and the other a lowland region. Censuses made at both sites indicated that the majority of the birds did not attempt to breed and that annual recruitment came from 30 to 40% of the population. Individual females tended to lay more eggs in the lowlands, with a mean clutch-size of 4.7 eggs, compared with 3·8 eggs per clutch in the highlands. A mean brood-size of 3.1 cygnets was obtained at both the highland and the lowland sites in August but the highland cygnets were significantly smaller and lighter. The difference in cygnet size could be attributable to one or a combination of factors including age differences and habitat variables. Lowland adults were significantly heavier than those from the highlands, which reinforced the view that habitat quality was superior at the lowland site. There was no difference in the feather length recorded for adult swans moulting in the two study areas, indicating that the moult occurred concurrently in the highlands and lowlands. The number of cygnets lost per brood between ringing and resighting in the wintering range was significantly higher for the highland swans, although the number of highland families relocated was small. The results indicate that birds from different breeding areas may contribute disproportionately to the percentage of juveniles reared annually in the population.

Detailed studies of fecundity and juvenile survival rates in migratory Anatidae have described a number of factors that influence reproductive success, both for individual birds and for the population as a whole. However, comparatively few authors have monitored the success of individual pairs throughout the breeding season with a view to estimating juvenile survival rate at different stages of their development. Moreover, the level of juvenile mortality during autumn migration has received little attention due to difficulties in relocating individual birds in the wintering range, although this factor is likely to be important in limiting the growth of the population (Owen & Black 1991). In addition to having a direct effect upon population size, fluctuations in juvenile survival rates influence the age structure of the population, which may in turn influence recruitment to the breeding population.

The Whooper Swan *Cygnus cygnus* is a migratory species that breeds at latitudes of between 45°N and 70°N, extending from Iceland and northern Scandinavia across the USSR to the Pacific coast (Ogilvie 1972). The swans migrate south each autumn and reports of individuals marked with plastic leg-rings have shown that birds wintering in Britain and Ireland are mainly from the Icelandic breeding population (Brazil 1983, Black & Rees 1984, Gardarsson 1991), with only limited interchange with those occurring on the continental mainland. The percentage of juveniles recorded in Britain between 1948 and 1984 ranged from 5% to 26%, with a mean value of 19.6% (Salmon & Black 1986), but little is known of the factors affecting the breeding success of the population. Moreover, although Whooper Swans nest near marshy pools throughout Iceland, at altitudes ranging from sea-level to about 700 m (Gardarsson & Skarphedinsson 1984), the question of whether birds from different breeding regions contribute disproportionately to the percentage of juveniles raised each year has not previously been considered.

This study compares the breeding success of Whooper Swans from two geographically discrete areas of Iceland, one an upland region and the other at sea-level, to determine whether differences in habitat may be associated with reproductive success. The proportion of breeding birds was calculated, the survival rate for the cygnets at each stage of their development monitored, and the level of juvenile mortality during autumn migration assessed, in order to determine the relative importance of these variables in limiting annual recruitment to the population.

METHODS

Two main study areas were chosen: Skagafjörður in northern Iceland (65°40'N 19°30'W) and Jokuldalsheidi in the

north east (65°14'N 15°30'W), each known to hold at least 30 breeding pairs of Whooper Swans. Skagafjörður is a lowland coastal site of some 250 km^2, consisting of grazed pasture and marshes in and around the Heradsvotn delta. Jokuldalsheidi in the highlands extends to 340 km^2 of glacial deposits studded with bogs and marshy areas, with abundant lakes and small pools.

An aerial survey of Skagafjörður was made on 11 May 1988 to record the total number and distribution of swans in the area. Nests were then visited from 12 to 31 May 1988 to determine the final clutch-size for each pair; in four cases the eggs were cold, indicating that incubation had not started and that the clutches were probably incomplete. The maximum length and width of each egg was measured with calipers; fresh eggs were weighed on a 500 g Pesola balance. Egg volume was calculated using the formula:

$$\text{Volume} = \text{Length} \times \text{Breadth}^2 \times K_v$$

where K_v is a constant of 0.512 for swan eggs (Stonehouse 1966, Hoyt 1979). A small number of ringed swans present at Skagafjörður had been previously caught in Britain and Iceland and marked with plastic leg-rings, each engraved with a three letter code, which could be read at distances of up to 300 m with a telescope (Ogilvie 1972, Rees *et al.* 1990a). The remainder were identified by drawing their black and yellow bill patterns, which can be used to distinguish between individual birds (Brazil 1981, Rees 1981). Thus it was possible to trace the different pairs, together with their offspring, upon returning to Skagafjörður in mid-summer.

Jokuldalsheidi was covered with ice and snow for most of May and the swans did not start laying until the end of the month. Nests were visited between 10 and 21 June, however, and final clutch-size was recorded in each case. Information concerning egg-size was not collected in the highlands for logistical reasons resulting from the late start to the breeding season.

The breeding pairs were relocated on their territories between 5 and 19 August and the number of cygnets present in each brood was counted. The families were then caught and each swan was marked with a plastic leg-ring, engraved with a three letter code, to aid identification in the wintering range (Fig. 1). An Icelandic Museum metal ring was fitted to the other leg. The swans were weighed and linear measurements were made of the skull, tarsus and second primary feather (eventually the longest). Sex was determined by cloacal examination; the presence of any tape-worms in the vent was recorded for an assessment of whether parasitic infestation might influence cygnet survival rates. Photographs were taken of the bill markings of the adult swans for comparison with the drawings made in the spring. Non-breeding birds, mostly found in large moulting flocks, were also caught so that their body-mass and feather growth might be compared with the biometrical data recorded for breeding pairs, and to augment the number of marked swans in the population.

The estimate of the number of cygnets lost per brood during autumn migration was based mainly upon reports of families identified by ring number in Britain and Ireland during the 1988–89 winter, since juvenile Whooper Swans normally associate with their parents during the first winter. Additional information concerning swans resighted up to spring 1990 were included in an overall analysis of the survival of cygnets from the different sites. The two Icelandic study areas were revisited in August 1989 to determine the breeding success for birds nesting at each site for a second season and to identify marked birds returning to their breeding or natal areas.

Figure 1. Whooper Swan family (two adults and four cygnets) awaiting release after ringing.

RESULTS

Proportion of breeding birds in the two study areas

A total of 378 Whooper Swans was found in Skagafjörður during the aerial survey on 11 May 1988; 54 (14.3%) of these individuals were paired and in close proximity to a nest mound; a further 72 (19.0%) paired birds occurred on discrete marshy pools but apparently were without a nest; and the remaining 252 (66.7%) were recorded in groups or as single birds (Table 1). However, observations made on the ground from 12 to 31 May indicated that pairs were still prospecting for suitable nest sites with the movement of birds about the marshes causing frequent territorial disputes. By the end of the month the number of birds with clutches had risen to 96 (25.4%). The non-breeding flocks concentrated either on areas of open water, such as lake Miklavatn and the main Heradsvotn river channel, or in agricultural drainage ditches (Fig. 2).

Only 238 individual swans were found in the Skagafjörður area in mid-summer, including 49 in a flock on lake Vatnshlidarvatn, 10 km west of the Skagafjörður valley. Two pairs, identified by ring number, that had laid eggs but were unsuccessful at Skagafjörður in the spring were subsequently caught at Vatnshlidarvatn, confirming that some of the unsuccessful breeding pairs moved to this site to moult. Data obtained from the two sites therefore have been combined. Of the 238 swans in the area, 94 (39.5%) were recorded as paired and 74 (78.7%) of these were seen with cygnets (Table 1). Eight of the pairs that failed to breed either remained on their breeding territories or moved to larger moulting flocks where they were identified by ring codes. Two other pairs, recorded with eggs in spring, were relocated on their territories but the presence or absence of cygnets could not be ascertained.

The summer survey of the swans at Jokuldalsheidi similarly showed that, of the 235 swans counted in the area, 92 (39.1%) were recorded as paired and 72 (78.3%) of these were with cygnets (Table 1). The August censuses suggest, therefore, that 60.5% of the swans at Skagafjörður and 60.9% of the swans at Jokuldalsheidi had not attempted to breed, and that annual recruitment was dependent upon the breeding success of only 30–40% of the population. There was no significant difference between the two study areas in the number of birds recorded as paired or unpaired ($\chi^2_1 = 0.02$, n.s.).

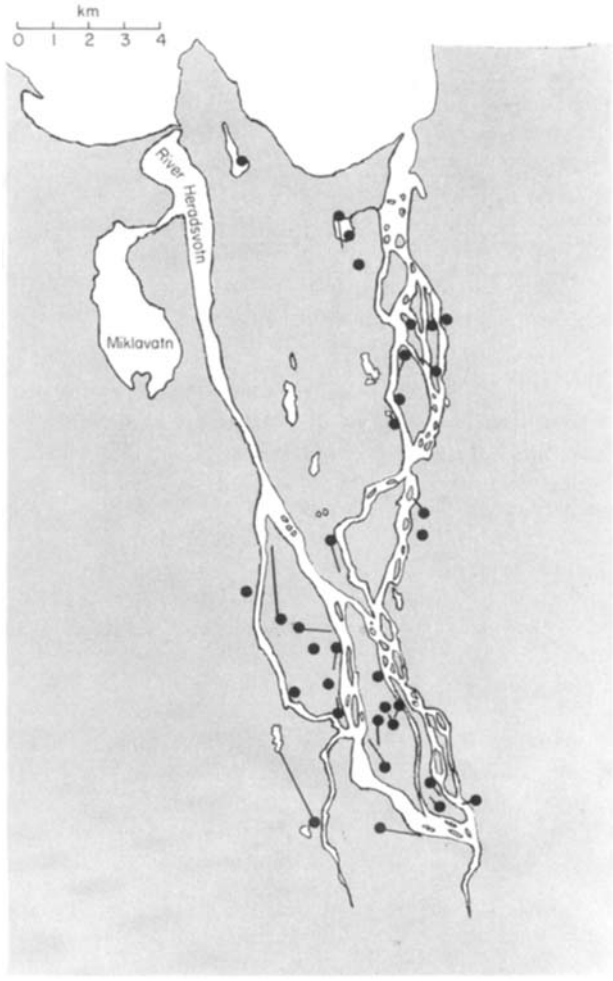

Figure 2. The distribution of Whooper Swan nests at Skagafjörður in May, showing where the families were relocated in August.

Table 1. *Population structure of Whooper Swans at Skagafjörður, Iceland, in spring and summer 1988, and at Jokuldalsheidi, Iceland, in summer 1988*

	Skagafjörður				Jokuldalsheidi	
	May 1988		August 1988		August 1989	
No. of birds	*n*	(%)	*n*	(%)	*n*	(%)
Paired swans	126	(33.3)	94	(39.5)	92	(39.1)
(i) recorded with eggs/cygnets	54	(14.3)	74	(31.1)	72	(30.6)
(ii) where eggs/cygnets were not found	72	(19.0)	20	(8.4)	20	(8.5)
Single swans	14	(3.7)	144	(60.5)	3	(1·3)
Groups	238	(63.0)			140	(59.6)
Total	378		238		235	

The summer 1988 count of swans in Skagafjörður was 140 birds less than had been counted in the spring that year, representing a decline of 37.0% of the population. The difference was mainly due to the decrease in the number of birds in flocks, despite a movement of some failed breeders to the group on Vatnshlidarvatn during the summer. It seems likely, therefore, that some of the birds present in spring were waiting at Skagafjörður for the highlands to thaw before proceeding to their upland nest sites.

Breeding success in the two study areas

Clutch-size and composition

Mean clutch-size (±s.d.) was 4.7 (±1.1) eggs at Skagafjörður and 3.8 (±0.8) eggs at Jokuldalsheidi (Fig. 3; $n_1 = 35$, $n_2 = 49$, Mann-Whitney *U*-test: $U = 1262$, $P < 0.001$, two-tailed test). The modal clutch-size was of five eggs in the lowlands and four eggs in the highlands, with nests containing more than five eggs found only at Skagafjörður.

Analysis of variance showed that the variation in egg dimensions was significantly less within clutches than between clutches (Table 2). Moreover, females that laid larger clutches also tended to produce larger eggs ($r_{150} = 0.02$, $P = 0.80$ for length, but $r_{150} = 0.25$, $P = 0.002$ for width and $r_{150} = 0.21$, $P = 0.01$ for volume, linear regression analysis). The mean mass (±s.d.) of 24 fresh eggs was 304 g (±20.0).

It was possible to calculate the date on which the first egg of the clutch was laid, assuming that the female laid one egg every 36 hours, for eleven pairs at Skagafjörður that had not commenced incubation when their nests were first visited, but there was no correlation between the onset of laying and the final clutch-size ($r_s = -0.05$, $n = 11$, $P > 0.90$, Spearman rank correlation).

Table 2. *Analysis of variance in the weight and dimensions of 152 Whooper Swan eggs laid in 35 clutches inspected at Skagafjörður, Iceland in May 1988*

	Length (cm)	Breadth (cm)	Volume (ml)
n	152	152	152
Mean	11.28	7.15	295.57
Range	10.16–12.15	6.51–7.73	231.86–351.83
s.d.	0.39	0.23	22.17
$F_{33,115}$	7.70	11.64	9.02
P	<0.001	<0.001	<0.001

Significance levels are for between *vs* within clutch comparisons.

Brood-size and juvenile growth rate

The mean brood size was 3.1 cygnets both at Skagafjörður and at Jokuldalsheidi in August 1988 (s.d. = 1.23 and s.d. = 1.06, respectively, see Fig. 3). Comparisons made of the weight, skull, tarsus and second primary measurements for cygnets caught at the two sites, however, showed that although the Skagafjörður cygnets were caught on average one week earlier than those in the highlands, the highland birds were still significantly lighter and smaller for each

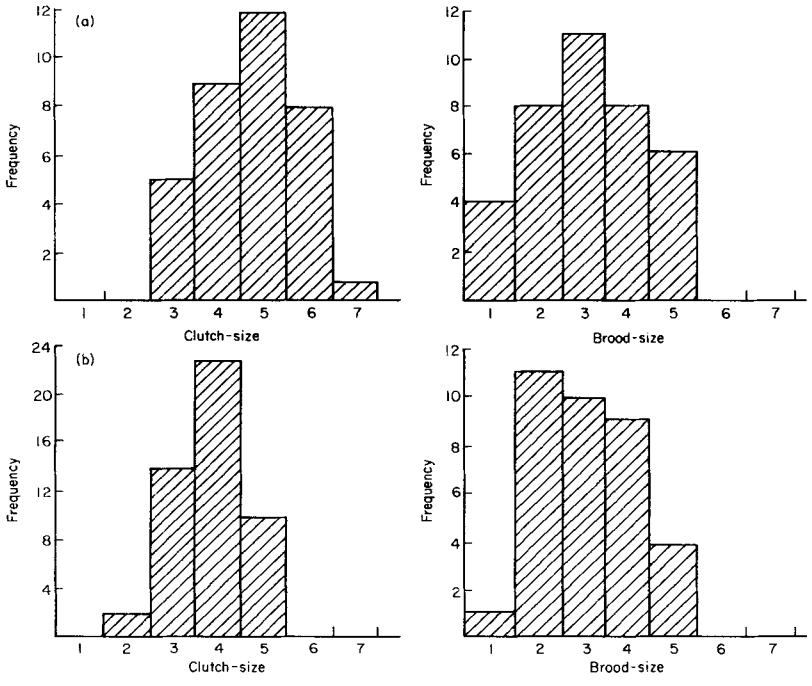

Figure 3. A comparison of clutch and brood sizes of Whooper Swans recorded (a) at the Skagafjörður lowlands and (b) at the Jokuldalsheidi highlands.

Table 3. *A comparison of the weights and measurements for Whooper Swan cygnets at Skagafjörður (lowlands), 5–10 August 1988, and Jokuldalsheidi (highlands) 14–19 August 1988*

		Weight (kg)			Skull-length (mm)			Tarsus-length (mm)			Second primary (cm)		
	n	Mean	Range	s.e.	Mean	Range	s.e.	Mean	Range	s.e.	Mean	Range	s.e.
Skagafjörður	82	5.2	2.4–8.2	0.13	142.3	110.8–168.6	1.36	110.9	80.0–130.2	1.15	6.8	0–23.8	0.72
Jokuldalsheidi	73	4.5	2.8–6.4	0.08	138.1	122.1–153.7	0.90	106.0	88.3–119.4	0.90	5.1	0–13.6	0.51
Mann-Whitney *U*-value			4263			3810			4032			3643	
P			<0.001			0.003			<0.001			0.016	

parameter considered (Table 3). The differences in the size of cygnets in the two study areas during early August 1988 could be due to one or a combination of factors including hatching date and habitat quality.

Observations made at Skagafjörður the following summer, in August 1989, found a mean brood size of 3.2 cygnets ($n=25$) in the area, which was similar to the 1988 results. The spring thaw at Jokuldalsheidi was even later in 1989 than in 1988, however, with snow still covering the site in June. The mean brood-size at Jokuldalsheidi in August was correspondingly low at 2.5 cygnets per family ($n=17$), which suggests that the breeding success of the swans in the highlands is more likely to be affected by annual fluctuations in weather conditions than at more temperate lowland sites.

Adult moult phase

There was no significant difference in the primary feather length recorded for adult swans from the two study areas ($U=99.5$, $n_1=14$, $n_2=16$, and $U=83.5$, $n_1=14$, $n_2=16$ for breeding males and females respectively; $U=685$, $n_1=22$, $n_2=55$, and $U=364$, $n_1=21$ $n_2=48$ for non-breeding males and females respectively; $P>0.05$ in each case; Table 4), indicating that the annual moult occurred concurrently in both the highlands and the lowlands. There was also no evidence to suggest that feather growth for non-breeders was more advanced than for breeding birds (Table 4) which differs from Owen & Ogilvie (1979), who found that non-breeding geese moult early, perhaps to increase the time available to lay down pre-migratory reserves. Female parents had longer primaries than did male parents (Table 4), indicating that the swans' moult period is staggered, with the female usually first to lose and re-grow her feathers. Non-breeding females also had significantly longer primaries than males in the highlands but not in the lowlands (Table 4).

Breeding birds tended to be heavier than non-breeders, and this proved statistically significant for male swans in the highlands (Mann-Whitney $U=838$, $P<0.001$; Table 5). Breeding females in the lowlands differed from this trend, however, by being significantly lighter than females without young ($U=101$, $P=0.04$; Table 5). The lowland swans were significantly heavier than those from the highlands when

Table 4. *Comparison of the lengths of primary feathers recorded for adult Whooper Swans from Skagafjörður (lowlands) and Jokuldalsheidi (highlands), Iceland*

	Breeding birds				Non-breeders				Breeding-status comparisons	
	n	Mean	Range	s.e.	*n*	Mean	Range	s.e.	*U*	*P*
Skagafjörður										
Males	14	7.7	0–19.6	1.6	22	10.7	0–15.3	1.2	96.5	<0.1
Females	16	14.3	0–24.5	2.0	21	11.7	0–31.0	1.8	128.0	n.s.
U (sex comparisons)			53				227			
P			<0.02				n.s.			
Jokuldalsheidi										
Males	16	9.2	0–25.3	1.9	55	11.7	0–24.7	1.9	365.5	n.s.
Females	14	17.1	0–28.8	2.7	48	15.3	0–37.2	2.1	245.5	n.s.
U (sex comparisons)			56				1015			
P			<0.02				0.04			

N.B. Four swans that had not moulted their old primaries were excluded from the analyses.

Table 5. *Comparison of the weights (kg) recorded for breeding and non-breeding Whooper Swans at Skagafjörður (lowlands) and Jokuldalsheidi (highlands), Iceland*

	Skagafjörður				Jokuldalsheidi				Site comparisons	
	n	Mean	Range	s.e.	*n*	Mean	Range	s.e.	*U*	*P*
Male swans										
Breeders	14	10.61	9.6–11.5	0.13	16	10.44	9.2–12.3	0.19	83.5	n.s.
Non-breeders	22	10.32	10.3–11.5	0.15	57	9.15	8.0–10.5	0.08	135.5	<0.001
U (breeding-status comparisons)			190				838			
P			n.s.				<0.001			
Female swans										
Breeders	16	8.69	7.6–11.0	0.18	14	8.07	6.4–10.5	0.27	61.0	<0.05
Non-breeders	21	8.89	8.0–9.8	0.09	48	7.76	6.7–8.7	0.18	47.0	<0.001
U (breeding-status comparisons)			101				398			
P			0.04				n.s.			

birds of different breeding status were considered separately ($U=61$, $P<0.05$ for breeding females; $U=135.5$ and $U=47.0$ for non-breeding males and females respectively, $P<0.001$; Table 5), which suggests that habitat quality was superior at the lowland site. Breeding males from the lowlands also tended to be heavier than those from the highlands but the results did not reach statistical significance, perhaps because the sample size was comparatively small (Table 5).

Success of individual pairs

Once the cygnets hatched, the families did not always remain in the vicinity of the nest site but moved to an adjacent marsh originally occupied by another pair. One family moved 3 km to feed when the marsh surrounding the nest site dried out during the summer months (see Fig. 2). A comparison of clutch-size with subsequent brood-size for the 26 pairs that were relocated in the summer indicated that, although pairs with three eggs lost on average fewer eggs or cygnets by August than pairs with six eggs (mean number lost being 0.5 cygnets/clutch and 1.5 cygnets/clutch, respectively, Fig. 4), there was still a positive association between clutch-size and brood-size ($r_s=0.47$, $n=26$, $P<0.01$, Spearman Rank Correlation, Fig. 4). Moreover, birds recorded with five or six eggs in spring did not lose significantly more eggs or cygnets by August than birds with smaller clutches ($\chi^2_1=0.23$, n.s.; Fig. 4).

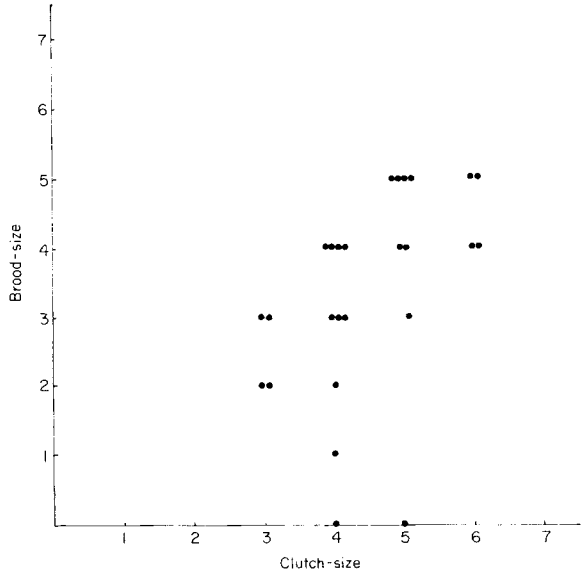

Figure 4. Correlation between clutch size and brood size in summer for individual pairs of Whooper Swans nesting at Skagafjörður ($r_s=0.47$, $n=26$, $P<0.01$).

Post-fledging survival

A total of 25 families (including 80 cygnets) was ringed at Skagafjörður and 23 families (including 70 cygnets) at Jokuldalsheidi. A further two cygnets from the lowlands and three from the highlands that were caught and measured were found to be too small to mark with leg-rings. Adults and juveniles from 15 (60%) of the lowland families were reported in Britain or Ireland during the 1988–89 winter, and juveniles from 21 (84%) of the lowland families were sighted by spring 1990. By comparison, only seven (30.4%) of the highland families were recorded in the wintering range in 1988–89, with juveniles from 11 (47.8%) of the highland broods sighted by spring 1990. Forty-eight (60%) of Skagafjörður cygnets but only 15 (21.4%) of Jokuldalsheidi cygnets were identified by ring number during or after the 1988–89 winter ($\chi^2_1=22.84$, $P<0.001$, Table 6). There was no apparent difference between study areas in the number of

Table 6. *Survival of ringed Whooper Swans*

	Skagafjörður		Jokuldalsheidi			
	n	(%)	*n*	(%)	χ^2	*P*
Families ringed	25		23			
Families seen in 1988–89 winter	15	(60.0)	7	(30.4)	4.31	<0.05
Family members resighted by 1991	21	(84.0)	11	(47.8)	7.11	<0.05
Cygnets ringed	80		70			
Cygnets seen in 1988–89 winter	30	(37.5)	11	(15.7)	9.14	<0.01
Cygnets resighted by spring 1991	48	(60.0)	15	(21.4)	22.84	<0.001
Adults ringed	75		136			
Adults seen in 1988–89 winter	23	(30.7)	41	(30.1)	0.08	n.s.
Adults resighted by spring 1991	57	(77.0)	72	(52.9)	10.91	<0.001

adult birds sighted in Britain and Ireland during the 1988–89 season ($\chi^2_1 = 0.80$, $P > 0.05$ for breeding birds and $\chi^2_1 = 0.03$, $P > 0.05$ for non-breeders, Table 6), which suggests that there was no bias in the reporting in the wintering range of birds ringed at the two sites. Significantly more adults ringed in the lowlands had been resighted by spring 1990 (Table 6), but this may be attributed to the low number of birds present at Jokuldalsheidi in August 1989; only 136 swans (excluding cygnets) were found in the area compared with 235 in August 1988.

The mean brood-size recorded for the ringed families during the 1988–89 winter, when cygnets hatched in 1988 were still expected to be associating with their parents, was 2.3 cygnets per brood ($n = 15$) for the lowland families, and only 1.4 cygnets per brood ($n = 7$) for those from Jokuldalsheidi (Fig. 5). Further analysis of these 22 families confirmed that the number of cygnets lost per brood between ringing and resighting was significantly higher for the highland swans (mean number lost $\pm$ s.e. $= 0.67 \pm 0.22$ for Skagafjörður and 2.57 ± 0.30 for Jokuldalsheidi, $U = 4$, $P < 0.002$ Mann-Whitney *U*-test). Seven complete families, where the cygnets all survived autumn migration and were resighted in the wintering range, all came from the lowland site.

Juveniles from Skagafjörður subsequently seen in the wintering range were not significantly larger or heavier in early August than members of the same brood that were not seen in winter ($t_{15} = 0.91$; $t_{15} = 1.02$; $t_{12} = 1.0$; and $t_{17} = 0.66$; two-sample *t*-tests for weight, skull-length, tarsus-length and primary feather length respectively, n.s. in each case). The variation in biometrical data shortly after hatching is likely to be influenced by the age of the cygnets but it was not possible to control for this factor since, in most cases, the hatching date was not known. The presence or absence of tape-worms in the digestive tract (detected whilst determining the sex of the swan) did not appear to affect cygnet survival rate; of 29 cygnets with tape-worms 11 (37.9%) were resighted in winter, and of 121 cygnets apparently without tape-worms 29 (24.0%) were subsequently seen in the British Isles ($\chi^2_1 = 2.19$, n.s.).

There was a strong correlation between brood size in August and the number of cygnets from each family known to have survived autumn migration for families marked in the lowlands ($r_s = 0.69$ $n = 15$, $P < 0.001$; Fig. 5). A similar association between summer brood-size and the number of cygnets resighted the following winter was not statistically significant for the highland families, but the sample size was small ($r_s = 0.69$, $n = 7$, n.s.; Fig. 5). The number of cygnets in the family in August was not associated with the number missing from the brood during the following winter ($r_s = -0.26$, $n = 15$ for Skagafjörður families and $r_s = 0.39$, $n = 7$ for Jokuldalsheidi families, n.s. in each case). A comparison of clutch-size with winter brood-size for the 12 Skagafjörður families that yielded data for each stage of the cygnets' development confirmed that birds that laid more eggs were accompanied by more offspring in the wintering range ($r_s = 0.73$, $n = 12$, $P < 0.01$).

DISCUSSION

One of the first requirements in evaluating the factors influencing the breeding success of a population is to determine the proportion of pairs that attempt to breed and the proportion that succeed in raising broods each season. The intensive survey of the Skagafjörður lowlands in August 1988 found only 94 paired swans in the area (representing 39.5% of the birds present), of which at least 82 (87.2%) had been recorded with eggs in the spring and 74 (78.7%) were resighted with young. Similarly, 143 (60.9%) of the 235 swans recorded in the highlands in August were recorded as single birds or in non-breeding flocks. These results agree with Gardarsson & Skarphedinsson (1984), whose aerial survey of breeding habitat in north, south and south-west Iceland in August 1982 found that 30% of the swans were in discrete pairs, compared with 70% in moulting flocks, and that 61% of the pairs had raised young. It seems therefore that a large proportion of the population does not attempt to breed; it remains to be seen whether this is due to one or a

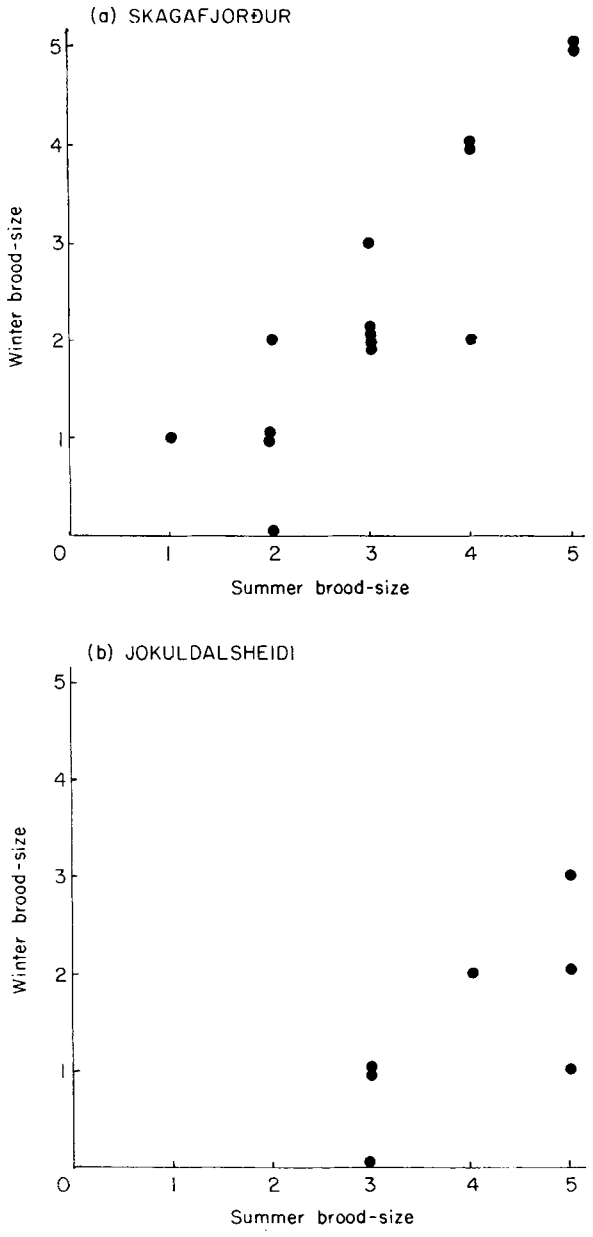

Figure 5. Correlations between summer and winter brood sizes recorded for Whooper Swan families that nested at (a) Skagafjörður ($r=0.88$, $n=15$, $P<0.001$) and (b) Jokuldalsheidi ($r=0.68$, $n=7$, n.s.).

combination of variables including habitat constraints and the proportion of young birds in the non-breeding flocks. The proportion of breeding adults was found to be similarly low in the Solway–Spitsbergen Barnacle Goose *Branta leucopsis* population where only 40% of the mature pairs nested in 1986 (Owen & Black 1989a). The decline in the percentage of breeding Barnacle Goose pairs and juveniles recorded between 1970 and 1986 appeared to be a function of the increase in size of the population during this period (Owen & Black 1989b).

The comparison of the breeding success for pairs from the two study areas in 1988 showed that the lowland swans laid larger clutches, the development of their cygnets was more advanced by August, and a higher proportion of lowland cygnets were recorded in the wintering range. The variation in breeding success between the two study areas could be due to a number of factors, including climatic conditions and food supply, both before and after the eggs were laid. Although there was no correlation between laying date and final clutch-size at Skagafjörður, the late start to the breeding season attributable to adverse weather conditions in the highlands may still have been responsible for the smaller clutches found at Jokuldalsheidi. Clutch-size diminishes as the season progresses in Mute Swans *Cygnus olor* (Reynolds 1972) which may advance the hatching date for late breeders by several days. The low mean brood-size recorded at Jokuldalsheidi in August 1989, following a spring thaw even later than in 1988, reinforces the view that the breeding success of pairs nesting in the highlands each year is particularly susceptible to fluctuations in weather conditions. Even if the smaller size of the highland cygnets is due to relative age alone, however, the fact that the Jokuldalsheidi cygnets were less well advanced than those from the lowlands by mid-summer could, in turn, affect their preparedness for autumn migration and subsequent survival. It remains to be seen whether the reproductive performance of swans in the more temperate lowlands is generally more consistent, and whether the annual variation in the percentage of juveniles recorded in the wintering population is due mainly to annual differences in the breeding success of swans from the highlands. Certainly the percentage of cygnets in the wintering population was low during the 1989–90 season (Rees *et al.* 1990b). A more detailed study of the swans' feeding ecology is also necessary to determine whether variation in the food supply also influences the reproductive success at different sites and in different years. Certainly the observation that the lowland adults were heavier than those from the highlands suggests that the habitat quality was superior at the lowland site.

Although post-fledging survival has been studied in few migratory species, juvenile mortality during autumn migration is generally considered to be high, particularly if the birds fly long distances over the sea to reach their wintering range (Owen & Black 1989b, 1991). The present study found that, in the case of the lowland-breeding swans, mean clutch-size was 4.7 eggs and mean brood-size was 3.1 cygnets, representing a loss of 34.0% of the potential offspring between May and August, with a further 0.67 cygnets (14.3% of the original clutch) missing by the time that the family were resighted in the wintering range. Other studies indicate that the annual mortality rate for migratory swans is less than 35% for birds in their second year, and less than 20% thereafter (Evans 1979, Scott 1988), so it seems that the most hazardous period for the lowland cygnets is the time prior to fledging. Similar results have been obtained for geese,

with the highest levels of gosling mortality occurring before the goslings reach the brood rearing sites (Prop *et al.* 1984). Survival rates for Whooper Swan cygnets proved different in the highlands, however; the mean clutch size (3.8 eggs) was smaller than in the lowlands but the mean brood size of 3.1 cygnets in August represented a loss of only 18.4% of potential offspring, which may be due to the cygnets having hatched more recently than those at Skagafjörður at the time of the survey. Only seven of the families ringed in the highlands were resighted in the wintering range, but the mean number of cygnets missing from these broods (2.43 juveniles) represented 63.9% of the original clutch. If the laying period for the highland swans is normally later than for those in the lowlands, then the autumn weather may have a significant effect upon the survival of cygnets from this region. Further research may determine whether underdeveloped cygnets, unable to migrate with the family party in autumn, are able to survive and continue their growth in mild winters and to migrate south at a later date. Owen & Black (1989b) showed that the smallest of the juvenile Barnacle Geese weighed and ringed at Spitsbergen in August 1986 failed to reach the wintering grounds that year. Although the present study found that the size and weight of cygnets at Skagafjörður in early August was not associated with survival into the first winter, hatching date and factors affecting juvenile growth rates may prove more critical in regions where the breeding season is delayed.

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