

Population composition, and return according to breeding status, of Bewick's Swans wintering at Slimbridge, 1963 to 1976

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When conservation measures produce a new refuge, or make an existing site attractive to a previously unrecorded species, numbers of birds may increase rapidly. While the management techniques responsible may be described, and the increases quantified, it has not been possible to investigate the structures of such new populations; individual identification of all the members of the population is required. Artificial marking is inadequate, for it is unlikely that every individual can be caught, and at any time new birds may enter the population.

This problem may be overcome by using natural markings, which, among Bewick's Swans *Cygnus columbianus bewickii*, were found to be sufficiently varied and permanent to allow annual identification of several hundred individuals for up to 13 years (Evans 1977).

Bewick's Swans breed in northern Siberia, and the western population winters mainly in the Netherlands, England, and Ireland. Sharp increases in numbers have occurred in three places in Britain and Ireland during the past 20 years: at the Ouse Washes (Cambridge/Norfolk), at the Wexford Wildfowl Reserve, Eire, and at the Wildfowl Trust, Slimbridge, Gloucestershire, where the present study was made.

Study area

From 1955–56 Bewick's Swans were present annually on the Severn Estuary near Slimbridge. Up to 1960–61 numbers were less than 16, but in the next two winters they exceeded 30. Ogilvie (1969) attributed the establishment of this tradition to the severe weather of those two winters.

In February 1964 the calls of three pinioned Bewick's Swans and four pinioned Whistling Swans *Cygnus c. columbianus* attracted 24 wild Bewick's Swans from the estuary on to a lake of about half a hectare within the perimeter fence of the Wildfowl Trust. The area was undisturbed, except for a warden distributing a food supplement of wheat or barley several times a day. Such protection and feeding were undoubtedly responsible for the subsequent increases in numbers to a point where the density of wild

birds (including geese, ducks, gulls, and coots) was much higher than in any natural site (Figure 1).

Methods

Every Bewick's Swan of second winter or older could be identified individually, both during one winter, and from one winter to another, by its unique pattern of black and yellow on its bill (Scott 1966; Evans 1977). Cygnets, which had rather ill-defined bill patterns, were identified in their first winter through their constant association with their parents. In subsequent winters they were recognized as having been at Slimbridge previously, either through their continued association with their parents (Evans, in press a), or through having been ringed in their first winter. During the study period 617 swans visiting the lake were caught and ringed with numbered metal rings issued by the British Trust for Ornithology, and, except for a few early in the study, also with plastic rings, 35 mm tall, with digits 15 mm high, which could be read with a telescope up to 300 metres (Ogilvie 1972).

The lake was watched daily each winter and every swan appearing recorded. Each bird, except for cygnets, could be categorized as either 'New' (i.e. with no known experience of Slimbridge), or 'Experienced' (i.e. with experience of Slimbridge in at least one previous winter). In addition seven classes of New swans were defined according to breeding status: (i) cygnet, (ii) single yearling (second-winter swan), (iii) single adult, (iv) paired bird, with a mate also New (v) paired bird with an Experienced mate, (vi) family bird (i.e. a paired bird with cygnets) with a New mate, (vii) family bird with an Experienced mate.

The investigations of the proportions of swans returning were made in terms of individual swans, for they involved following the same bird through more than one winter, during which time its class might change. However, when examining the annual population composition, 'units' were used. These consisted of (i) a single yearling, (ii) a single adult, (iii) a pair, (iv) a family (Evans, in press b). Although the units in the last two



Figure 1. The lake at feeding time. (E. E. Jackson)

cases consisted of more than one swan, paired and family birds normally stayed together, acting as one unit. Each of these four classes might be New or Experienced, although in the case of families 'Experienced' only applied to the parents, the cygnets obviously being New. Experienced pairs (or families) included pairs (or families) in which one bird was Experienced and one New. Among such pairs the influence of the Experienced bird predominated strongly, in, for example, timings of arrival and departure, or amounts of presence or absence from the area during the course of a winter (Evans 1978). The return proportions of the New birds in such pairs were similar to those of Experienced birds (see later).

Results

Annual numbers of units

The annual total of units recorded represented the number of different units visiting the lake during the course of each winter, as opposed to the maximum number seen on any one day.

Numbers of units increased from 12 (24

birds) in 1963–64 to 376 (570 birds) in 1969–70 (Figure 2). In 1970–71, a good breeding year, 626 birds were recorded, but the units numbered only 331. Annual numbers and the population structure detailed in numbers of swans, rather than of units, are given by Evans (in press a). As the sample in 1963–64 consisted of a very small number of units, all New, it was omitted from further consideration.

Annual proportions of classes

The proportions that New and Experienced yearlings represented in their respective categories correlated with the proportions of cygnets (Evans, in press a) the previous winter ($r = +.846$, $p < .01$, and $r = +.705$, $p < .05$ respectively). As the proportions of yearlings were thus dependent on previous breeding success, they were excluded from the examination of annual class proportions.

The proportions of the total New units each winter at Slimbridge represented by singles, pairs, and families are shown in Figure 3. In the nine winters from 1967–68 the proportion of families was only once

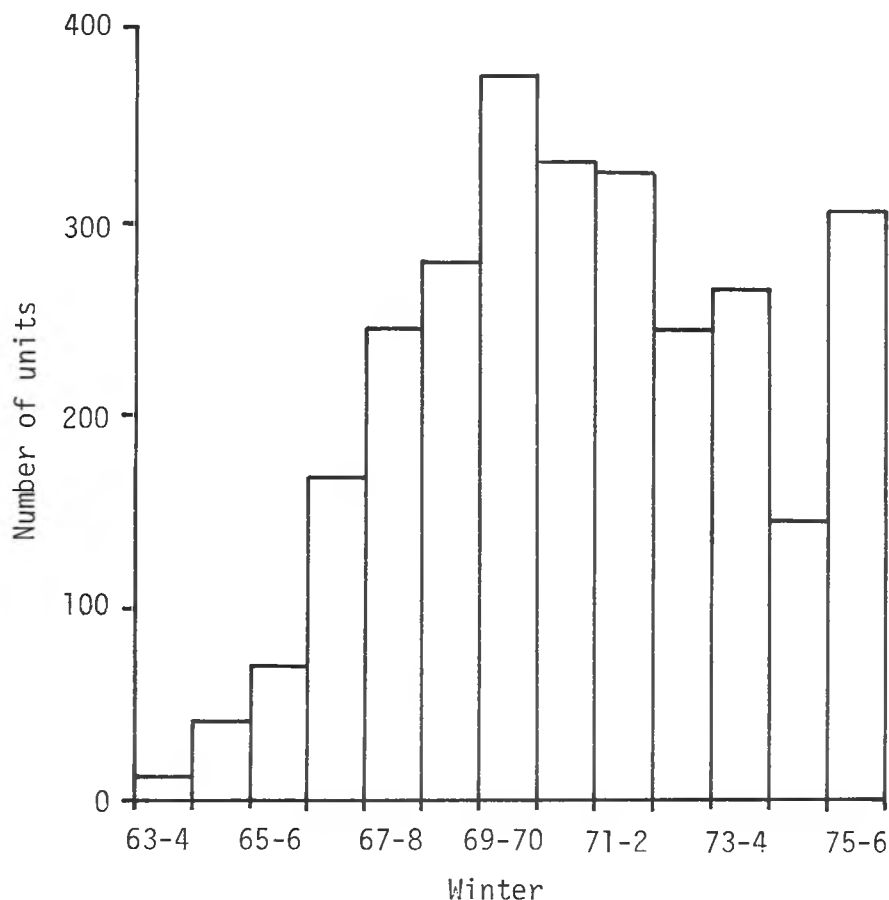


Figure 2. Numbers of swan units, 1963-64 to 1975-76.

above 8%, being 13% in 1972-73. In contrast the proportion of singles was always over 50%. The average proportions of the New classes over the 12 years were singles 59.7%, pairs 32.4%, and families 7.9%.

The proportions of Experienced singles, pairs and families were rather different from those of their respective New classes (Figure 4). The proportion of families was never less than 10%, and averaged 22.8%. Singles did not predominate, averaging 29.8%. Nearly half (47.4%) the Experienced units were pairs.

The class proportions in both categories were clearly different in the early years, when annual numbers were increasing, from what they were later in the study. Table 1 shows that major recruitment lasted to 1968-69, the proportions of New units always exceeding those of Experienced units. Thereafter the proportions of New units were never above 50%. Numbers in this second

period had probably stabilized, for annual unit totals varied directly according to climatic conditions (Evans 1979).

Table 1. Proportions of New and Experienced units (excluding yearlings), 1964-65 to 1975-76.

	Percentage New	Percentage Experienced
1964-65	75	25
1965-66	66	34
1966-67	52	48
1967-68	52	48
1968-69	61	39
1969-70	48	52
1970-71	35	65
1971-72	31	69
1972-73	30	70
1973-74	34	66
1974-75	27	73
1975-76	43	57

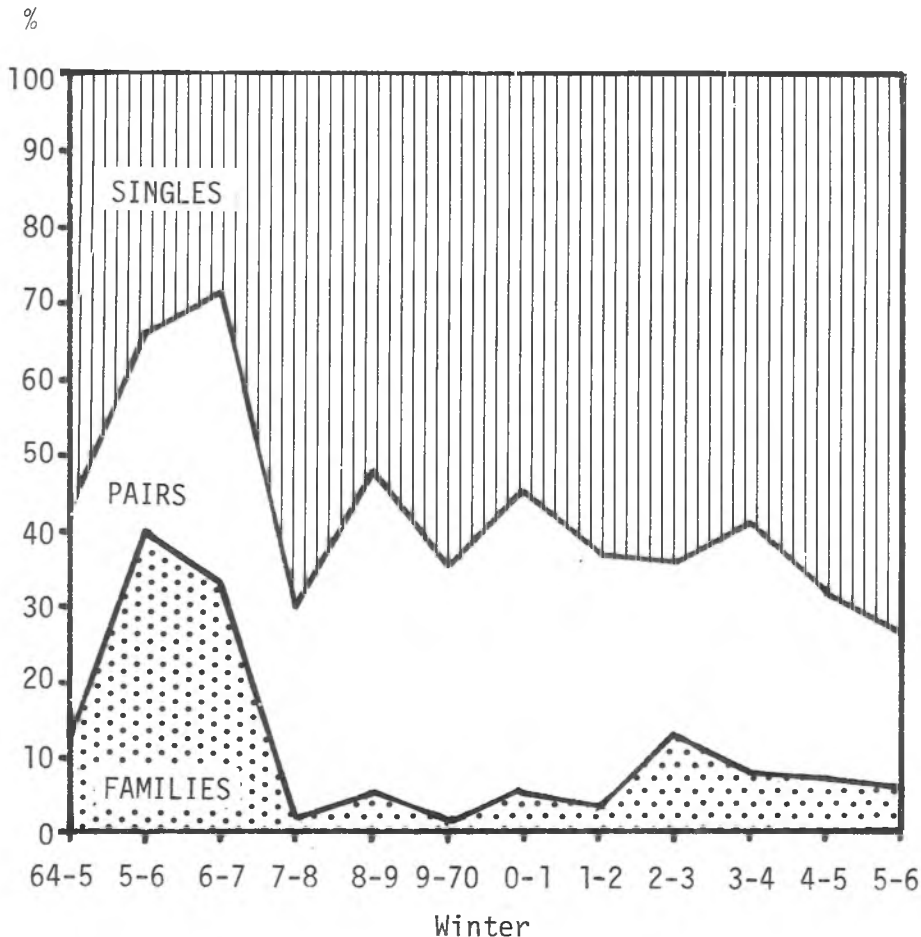


Figure 3. Annual proportions (%) of New singles, pairs, and families, 1964-65 to 1975-76.

The numbers of New and Experienced singles, pairs, and families during these two periods were compared (Figure 5). Up to 1968-69 numbers of New singles, pairs, and families were not significantly different from those of their Experienced counterparts (Mann-Whitney U test). After 1969-70, however, numbers of New and Experienced categories of pairs differed significantly ($p < .001$), as did those families.

Return of New birds, according to sex

The proportions of unpaired birds (i.e. cygnets, yearlings, and singles) recorded at Slimbridge between 1963-64 and 1974-75 that subsequently returned for at least one winter (although not necessarily that immediately following their first arrival) were

examined. Only the data on those birds caught and sexed cloacally were used, because sexing by observation of size and behaviour is very difficult in the case of unpaired birds.

The return proportions of males and females in each class showed no consistent trend, ranging from 32.0% for single females to 53.6% for yearling females (Table 2). The differences were not significant, either within each class, or overall (χ^2 test).

This agrees with the sexes of Experienced birds bringing New mates to Slimbridge during this period, rather than going to their partner's wintering site: 37 were males and 35 females. This was not significantly different from expected, based on the proportions of the sexes among single birds, 59.9% males: 40.1% females (Evans, in press a) (χ^2 test).

Return of New birds, according to class

As identification was sometimes by bill pattern, sometimes by ring number, the return proportions of ringed birds, recorded at Slimbridge between 1963-64 and 1974-75, were examined first, and then compared with those of unringed birds, in case any bias was present.

Table 3 shows the proportion of swans ringed during their first season at Slimbridge ($n = 412$), and of swans not so ringed ($n = 2,124$), that subsequently returned for at least one winter.

In most classes the proportion of ringed birds returning was higher than those unringed. This was to be expected, for the catching method selected out those birds

Table 2. Numbers and proportions of New unpaired swans returning, according to sex.

	Cygnets		Yearlings		Singles		Total	
	♂	♀	♂	♀	♂	♀	♂	♀
No. recorded	87	89	43	28	31	25	161	142
No. returning	35	29	17	15	16	8	68	52
% returning	40.2	32.6	39.5	53.6	51.6	32.0	42.2	36.6

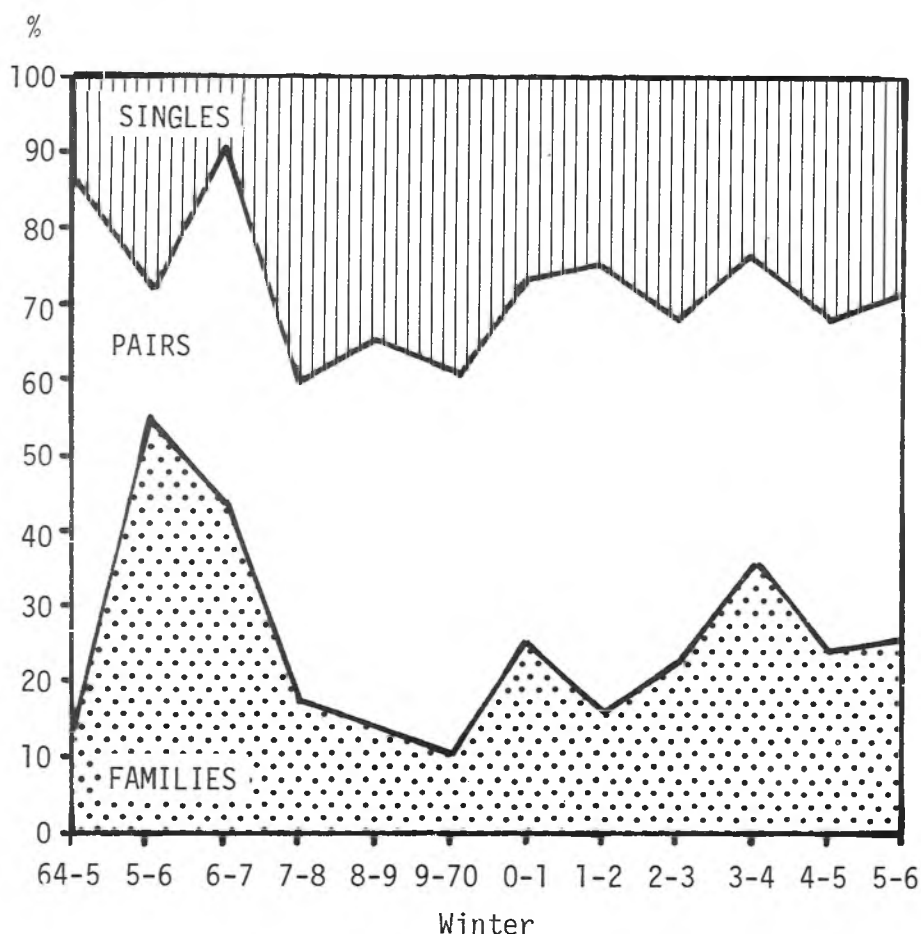


Figure 4. Annual proportions (%) of Experienced singles, pairs, and families, 1964-65 to 1975-76.

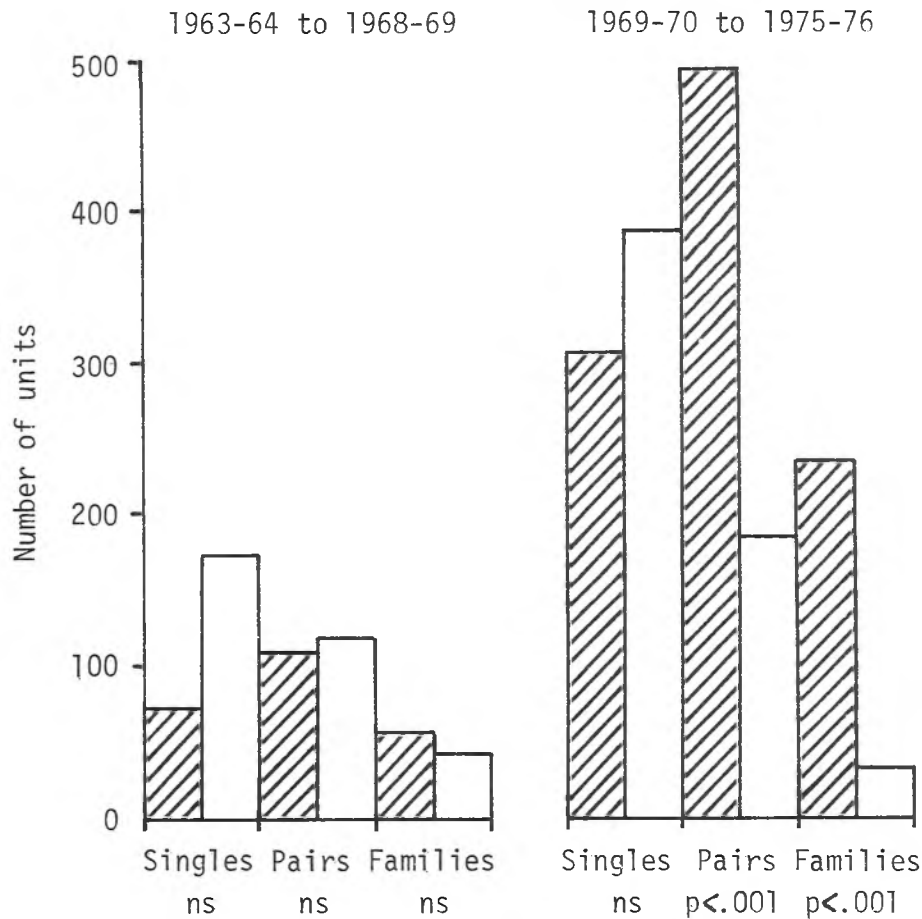


Figure 5. Numbers of New (plain columns) and Experienced (hatched columns) singles, pairs, and families from 1963-64 to 1968-69, and from 1969-70 to 1975-76. The statistical significance of differences between numbers of New and Experienced categories in each class, within each period, was tested by Mann-Whitney U test.

settled confidently enough on the lake to risk feeding in the confined channel in which they were caught. E.g. in 1970-71, the 24 New swans caught and ringed (excluding cygnets) stayed on average for 61 days, compared with only 12 days for the 108 other New swans not caught ($p < .001$; Mann-Whitney U test; swan units used). Birds that returned had stayed significantly longer previously than had the non-returning members of the same class (Evans, in press b).

Comparing within the ringed and unringed samples separately, the proportions of the unpaired birds (cygnets, yearlings, and singles) returning were very similar, with the exception of unringed cygnets. Differences were tested between pairs of classes according to age and experience, cygnets v.

yearlings and yearlings v. singles, but only the difference between unringed cygnets and yearlings was significant ($p < .05$; χ^2 test). The implication, that some unringed cygnets were not being identified on subsequent return, is not surprising. While they can be identified through associating with their parents in later years, their parents might not return, or cygnets might miss several winters and first return as paired birds.

The return proportions of paired birds, whose mates were also New, were significantly higher than those of unpaired birds in both ringed and unringed samples. They were not significantly different from those of family birds, with mates also New, in either sample.

The return proportions of paired birds first

Table 3. Numbers and proportions of classes returning in (i) ringed, (ii) unringed and (iii) total samples. The statistical significance of differences was tested by χ^2 .

Class	Cyg.		Yrlg.		Single		Paired (mate also New)		Paired (mate Experienced)		Family (mate also New)		Family (mate Experienced)
(i) Ringed in first season	176		77		61		41		45		8		4
% returning	34.1	/	41.6	/	36.1	xx	65.9	/	71.1		37.5	/	50.0
(ii) Not ringed in first season	535		345		426		531		148		121		18
% returning	10.5	x	15.9	/	18.3	xxx	31.6	xxx	58.8		35.5	/	50.0
(iii) Total	711		422		487		572		193		129		22
% returning	16.3		20.6		20.5		34.1		61.7		35.7		50.0

Not significant in ringed or unringed samples: Returns of

(i) Paired birds (mate also New) v. family birds (mate also New)

(ii) Paired birds (mate Experienced) v. family birds (mate Experienced)

Note: Significance levels entered between pairs tested; xxx $p < 0.001$, xx $p < 0.01$, x $p < 0.05$, / not significant.

Table 4. Numbers, recorded by classes, and proportions returning, from 1963–64 to 1968–69, and from 1969–70 to 1974–75. The statistical significance of differences was tested by χ^2 .

Class	Cyg.	Yrlg.	Single	Paired (mate also New)	Paired (mate Experienced)	Family (mate also New)		Family (mate Experienced)	Total
No. recorded 1963–64 to 1968–69	228	196	178	242	46	84		4	978
% returning	25.0	24.0	30.3	47.9	82.6	47.6	/	50.0	36.2
									xxx
No. recorded 1969–70 to 1974–75	483	226	309	330	147	45		18	1,558
% returning	12.2	17.7	14.9	23.9	55.1	13.3	xx	50.0	20.5

Note: Significance levels entered between pairs tested; xxx $p < 0.001$, xx $p < 0.01$, / not significant.

introduced by Experienced mates were even higher in both samples. Neither were significantly different from the return proportions of family birds introduced by Experienced mates.

Thus, in general, paired birds returned in higher proportions than unpaired ones, while, if the bird had been introduced by an Experienced mate, its return chances were increased further. It is, however, interesting that the differences between the return proportions of birds introduced by an Experienced mate and of birds whose mate was also New should be not significant in the ringed sample, and yet be so highly significant ($p < .001$) in the unringed.

The return proportion of unringed paired birds with Experienced mates seems abnormally high in comparison with those of the other unringed classes. However, as mentioned earlier, in pairs where one partner was Experienced, one New, the pair had a much longer attendance than any other of the New classes (Evans 1978). This probably explains their much higher proportion of return, together with the fact that most of them returned with their mates, which by then had spent at least two winters at Slimbridge. More experience at Slimbridge increased a swan's chances of return (see later).

Return proportions during first and second halves of the study

As the return proportions of ringed and unringed samples showed similar differences between the classes, further examinations of return proportions could be made on the total sample.

Table 4 shows the proportions of swans that subsequently returned, grouped according to their class in their first season at Slimbridge between 1963–64 and 1968–69 (during the build up), and between 1969–70 and 1974–75 (when numbers had stabilized).

Despite the continuity of observer in the second period, a decline in the returns is indicated. For all the classes combined it was only 20.5%, compared with 36.2% in the first period ($p < .001$, χ^2 test).

While the data in Table 4 generally show similar differences between the classes to those in Table 3, there were high return proportions of paired birds, with and without cygnets, in the first period. Also there was a very low return proportion of family birds where both parents were New to Slimbridge during the second period (13.3%). This was significantly different from that of family birds introduced by Experienced mates (50%; $p < .01$).

Return of Experienced birds

While only about a quarter of all the swans recorded between 1963–64 and 1974–75 returned for a second season, about two-thirds (65.3%) of those wintering a second time (i.e. Experienced birds) returned for a third time.

Table 5 shows third-winter returns divided according to whether the swan was first recorded in the build up period, 1963–64 to 1968–69, or subsequently, 1969–70 to 1973–74. During the first period, 36.2% of swans returned for a second winter, and the proportion of these returning for a third winter was 74.3%. In the second period, of the 21.4% swans returning for a second winter, 54.9% returned for a third. The differences between those returning for a second winter and those returning for a third were highly significant ($p < .001$, χ^2 test) in both periods.

The difference between the proportions of Experienced birds returning in the first and second periods was also highly significant ($p < .001$). Thus even these more 'committed' birds were less likely to return in the second period.

Table 5. Return proportions of New and Experienced birds. The statistical significance of differences was tested by χ^2 .

Period in which swan first recorded	No. (%) returning for second winter (i.e. New birds)		No. (%) returning for third winter (i.e. Experienced birds)
1963–64 to 1968–69	354 (36.2%)	xxx	263 (74.3%)
1969–70 to 1973–74	304 (21.4%)	xxx	167 (54.9%)

xxx = significant between pairs tested, $p < 0.001$.

Patterns of return

A swan recorded as returning to Slimbridge after its initial season might be present in consecutive winters, or there might be an interval of several winters between its visits.

Of the 674 birds returning, 431 (63.9%) returned in successive winters (up to 12) without a break. Table 6 shows the numbers and proportions of all returning swans that these represented. A quarter of all the birds returning came for one successive winter, and another quarter for two, three and four successive winters. Only 12.6% came for sequences of five winters or more.

One bird came for 13 winters (including his first), i.e. since the beginning of the study, and 17 swans came for ten or more winters. The records are, however, naturally biased against such long sequences, in that many birds first arrived in recent years.

Swans which had breaks of one or more winters between their appearances numbered 243. One winter was missed by 20.0% of all returning birds, while 5.9% missed two consecutive ones. The swans missing three, four or five consecutive winters each constituted less than 2.0% of the total (Table 7).

Nearly 7% of returning swans missed winters on two or even more occasions. For example, they missed a winter, returned, missed the next winter, and returned again. Table 7 also shows numbers and proportions of swans missing various combinations of winters, those other than 1 + 1 being fairly rare.

Some winters were missed by more birds than others. For example, 1969–70 was only missed by 10.7% of birds that subsequently returned, while 1974–75 was missed by 41.4% of birds returning the following winter. This was related to the amount of south to west winds each winter, high proportions of which inhibited large numbers of swans arriving (Evans 1979).

Discussion

Initial recruitment of swans to Slimbridge came from all the classes. By 1968–69 daily totals on the lake were regularly over 350, and, with the addition of hundreds of geese and ducks, it seems likely that saturation point was reached. Figure 1 shows that the density of wild birds was obviously un-

Table 6. Numbers of birds returning to Slimbridge in consecutive winters after their first appearance.

Winter first seen	No. winters after first appearance											
	1	2	3	4	5	6	7	8	9	10	11	12
1963–64	3	1	2	2	1	1	1	2	1			1
1964–65	2	3	1	2	1	2	1	1	1		1	
1965–66	14	4	2	3	1	2	1	3		8		
1966–67	18	7	5	4	2	3	4	2	5			
1967–68	5	6	5	7	2	3	1	2				
1968–69	32	18	16	8	8	1	6					
1969–70	22	9	8	7	3	11						
1970–71	25	5	6	3	3							
1971–72	20	7	3	5								
1972–73	12	3	14									
1973–74	5	6										
1974–75	16											
Total	174	69	62	41	21	23	14	10	7	8	1	1
% of all returning birds	25.8	10.2	9.2	6.1	3.1	3.4	2.0	1.5	1.0	1.2	0.2	0.2

Table 7. Numbers of swans missing winters at Slimbridge

	Number of consecutive years missed.					Combinations of years missed				
	1	2	3	4	5	1+1	1+2/ 2+1	1+3/ 3+1	1+4/ 4+1	1+1+1
Number of swans	135	40	12	8	2	27	11	3	2	3
% of all returning birds	20.0	5.9	1.8	1.2	0.3	4.0	1.6	0.5	0.3	0.5

natural, and this resulted in a much higher level of aggression than at more natural sites.

There were probably several reasons for subsequent recruitment being mainly through single birds. Among New birds, singles arrive considerably ahead of pairs, which in turn are ahead of families (Evans, in press b). This probably reflects the weaker attachment of singles (generally rather young birds) to a traditional wintering site than that of paired birds. The lake is less crowded earlier in the season, and thus less daunting.

The extremely low proportion of New families may arise from the later congestion. Frequently both Experienced and New families have difficulty landing their cygnets on first arrival. When the parents also cannot land, the family is most probably New, and after several futile attempts such families may fly away altogether. Probably they only come to Slimbridge in the first instance if forced by climatic conditions, but, being the last of all the classes to arrive, they find the lake already crowded with other refugees from the cold weather.

It seems therefore that the relatively small lake is not a suitable place for New families. Those that succeeded in landing stayed on average only 19 days, 62% of them departing within a week. This restlessness was reflected even among Experienced families, which had a greater amount of absence from Slimbridge than any of the other Experienced classes (Evans, in press b).

Of course, as the years pass, the pool of Experienced birds increases, with a bird's chances of return being affected generally by the length of its initial stay at Slimbridge, and particularly by its class then. The importance of each of these factors may vary: e.g. yearlings and singles, which returned in the lowest proportions, had longer average attendances (36 and 31 days) than New pairs (22 days) and families (19 days) (Evans, in press b); and cygnets, which also returned in low proportions, mostly had parents and consequently shared their relatively long attendances (62 days).

Cygnets, yearlings and singles therefore did comparatively well on the lake, so it was probably not their experience at Slimbridge which leads to low proportions returning. Unless they manage to rejoin their parents, the previous year's cygnets and yearlings have limited migration experience to find their way back alone. Singles may find a mate in the intervening summer, and go with them to their wintering site. This agrees with the finding of Boyd (1955) that Pink-footed

Geese *Anser brachyrhynchus* marked as goslings showed much less attachment to their region of marking in subsequent winters than did those marked as adults. Such 'wanderings' by younger birds may help to build up a useful knowledge of suitable wintering areas.

Having a mate significantly increased the chances of a swan's return to Slimbridge. Not only was the stimulus to go to Slimbridge reinforced by there being two birds instead of one, but they were older than cygnets, yearlings, and most singles, and thus had more experience of migration.

During the first period, the presence of cygnets with a New bird (whose mate was also New) did not affect its chances of return, but in the second period the return proportion of such family birds was poor, probably due to their very short experience of the lake.

Birds with the greatest chance of returning, however, were those introduced to Slimbridge by an Experienced mate. Indeed, their return proportions in the two periods were similar to those of Experienced birds coming for a third winter. The effect of experience is presumably cumulative. Swans coming for only one year may not have liked the place, and next year gone elsewhere. Those that return, however, must have found some attraction, which is reinforced by a second winter's stay.

The decline in the return proportion in the later, stabilized, period may be due to other sites becoming attractive, either because of favourable weather conditions farther east, or because other sites were improved and protected. Thus Bewick's Swans on the North Slob, Wexford, Eire, were scarce until the establishment of the Wexford Wildfowl Reserve in 1969, but reached 564 in December 1975 (Merne 1977). It may also be that it is not possible to make a proper comparison of returning proportions with the earlier years, for birds which have missed recent winters may yet return.

If identification is not annually reinforced, there is a greater possibility of a bird being wrongly classified as New when it does reappear. Ringing overcomes this problem but only 23% of swans were ringed up to 1973-74, and then not necessarily on their first visit to Slimbridge. Thus the proportion of a third of returning swans missing winters must be a minimum figure. Although there are advantages of wintering in a familiar area (Evans in press b) knowledge of alternative sites, as well as the ability to exploit new ones, must be important for survival.

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Summary

Bewick's Swans *Cygnus columbianus bewickii* were identified individually at Slimbridge from 1963 to 1976, both within and between winters, by bill markings or large numbered leg rings.

Each swan, except for cygnets, could be

categorized either New or Experienced. Seven breeding classes of New swans were defined for use in the analysis of return. Breeding units (four classes), rather than individuals, were used to examine the annual population composition.

Numbers of units increased from 12 in 1963–64 to 376 in 1969–70. Up to 1968–69 when numbers were building up, recruitment was from all the classes, but thereafter it was predominantly from single birds.

There was no significant difference between returning proportions of males and females. Significantly more ringed birds returned than unringed. Paired and family birds returned in higher proportions than single birds, but returning proportions were lower in all classes later in the study. Experienced birds were more likely to return than New ones. A third of returning birds missed one or more winters at Slimbridge.

Possible reasons for the above results are discussed.

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