Comparative demography of the swans: a review

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A wealth of new information on demography was presented at the Third International Swan Symposium. In this review, we attempt a first synthesis of this, and previously published, data. We emphasize parameters which have been estimated in many different studies. The estimates are summarized and compared, and we identify generalizations and hypotheses which can now be evaluated. We conclude with some tentative suggestions for standardizing collection of demographic data and with some speculation about which research areas are likely to generate the most exciting advances in our understanding of swan demography. As in the previous article, studies in this volume are referred to solely by the authors' name. We also utilize results from a questionnaire circulated at the Symposium asking investigators for their current estimates of several birth and death rates. Responses to this questionnaire are cited as personal communications from the respondents.

Demographic comparisons are best carried out by dividing the life cycle into a relatively small number of non-overlapping periods or events (e.g. Clutton-Brock 1988, Newton 1989). We used the following major categories in our analysis:

1. Per cent of adults breeding.
2. Average clutch size.
3. Survival from laying to adulthood.
4. Proportion of adults surviving each year.

The product of the first three terms (with clutch size divided by 2) is the number of adults entering the population each year; 1 minus the last term is the number of adults dying each year (with each quantity expressed as a proportion of the number of adults alive at the start of the year). In a stable population, births equal deaths so the product of the first three terms equals 1 minus the fourth term. Changes in population size of a few per cent per year (and few populations change more rapidly than that) may be ignored because the equality must still hold approximately. This fact means that any one of the terms can be estimated from the other three. We used this relationship to estimate survival from laying to adulthood because this component is difficult to estimate empirically.

We defined "adult" as birds ≥ 4.0 years old at the start of the breeding season. In one analysis we assumed that no birds younger than adults breed, though in fact a few younger birds probably do breed in many swan populations. Possible errors caused by assuming that birds

Table 1. Estimates of annual survival rates for swans ≥ 2.0 years old.

Species	Migratory?	Annual surv'l rates (%) Year 2	Year 3	Year 4*	Reference
Bewick's Swan	Yes	66	90	89	Rees (pers. comm.)
Tundra Swan	Yes	53	92	92	Nichols *et al.* (in prep.)
Whooper Swan	Yes	75	—	88	Haapanen
Trumpeter Swan	No	—	90	88	Anderson *et al.* (1986)
Mute Swan - Britain	No	62	67	81	Rees, Coleman (pers. comm)
Mute Swan - Denmark	No	74	78	80	Bacon & Andersen-Harild (1989)
Black Swan	No	78	78	84	Williams (1981)
Blk-nkd. Swan	No	—	—	—	—

younger than 4.0 do not breed are discussed below. We define birth as occurring when the egg is laid.

Adult survival rates

At least one estimate of adult survival rates is now available for each species except Black-necked and Coscoroba Swans (Table 1). When data were available we included survival rates for years 2 and 3. Where estimated mortality rates differed between sexes, we used the rate for females (because demographic analyses are usually based on rates for females).

The most obvious conclusion from the estimates in Table 1 is that all swan populations studied to date have extremely high survival rates compared to most avian species. Survival during year 2 appears to be 70-90% of adult survival rates. Survival in year 3 appears to be intermediate in some species but equal to adult rates in others.

The data suggest an interesting contrast between the migratory species and the relatively sedentary ones. The migratory species have higher adult survival rates, and subadults appear to attain these rates by year 3. In contrast, the sedentary species have markedly lower survival rates (note that the annual mortality of adult Mute Swans is nearly twice that of adults of the migratory species) and their survival rates during year three tend to be lower than adult rates. The Trumpeter Swan data in Table 1 constitute a partial exception to this generalization. Although the species is primarily migratory, the population studied to obtain the survival estimates is sedentary.

The causes of the differences between migratory and sedentary populations are at present obscure. The sedentary Mute Swan populations are both in industrial countryside where mortalities often occur due to collisions with overhead wires and from lead poisoning (Perrins, Coleman *et al.*, Sears & Hunt, O'Halloran *et al.*). Perhaps these problems, rather than migration *per se*, are responsible for some of the differences between migratory and sedentary species. It will therefore be interesting to obtain estimates of annual survival rates for Mute Swans in less built up areas, as well as for Black and Coscoroba Swans, and for additional populations of all species.

Adult survival rates are probably best estimated using modern capture-recapture methods which take account of failure to see all marked birds on each survey. For sedentary species, it is often possible to meet the assumptions of these methods, and in a few cases (e.g., Spray) it is even possible to census the population so that estimation methods are not needed. For the long distance migrants, however, immigration and emigration usually occur, which cause serious difficulty in capture-recapture analyses. This problem is best solved by distributing the surveys to resight birds over the entire population. This is usually only practical on the wintering grounds because extensive travel in the breeding grounds is too difficult and expensive. It seems worthwhile, therefore, to identify wintering areas for migratory swans such that few birds move from one area to another either within or between years.

Results presented at the Symposium suggest that the smallest number of wintering areas - defined so that there is little or no exchange of birds between them - is probably about a dozen. Whooper Swans have five or six such areas (Rees, Gardarsson, Mathiasson, Vinogradov & Auezov, Kondratiev). Tundra Swans (Limpert *et al.*, Bart *et al.*) and Bewick Swans (Rees & Bowler, Kondratiev) each have two distinct wintering areas. Migratory Trumpeter Swans have one to three areas depending on whether the small populations breeding in Canada are counted (McKelvey *et al.*). This is an area in which international collaboration could be of great value in providing new information about many aspects of swan biology and conservation.

We wish to make one other point using the age-specific survival rates. In the sections below, we emphasize the proportion of adults that breed (lay at least one egg) each year. This estimate can be obtained from estimates of the proportion of all birds that breed, and from estimates of survival rates. Given one survival rate for year two (p2), and a constant annual survival rate thereafter (p), the proportion of birds at the start of the breeding season less than b years old may be expressed as

$$p_y = 1 - \frac{p_2 p^{b-3}}{1 + p_2 - p}$$

As noted above, the survivorship data suggests that p_2 is probably 70-90% of p in most populations. We used this range of values for p_2 in estimating the proportion of birds at the start of the breeding season that are <b years old for b = 2 to 6 (Table 2). The proportion of birds younger than b does not depend much on whether p_2 is 70% or 90% of p (see Table 2). Thus, uncertainty over this value is not particularly serious for our analysis. To convert the proportion of all birds breeding to the proportion of

Table 2. Proportion of swans at the start of the breeding season that are less than b years old assuming survival rates are p_2 in year 2 and are constant (p) thereafter.

Age	p (p_2 = .7p)			p (p_2 = .9p)		
b	.80	.90	.95	.80	.90	.95
2	.02	.01	.01	.08	.04	.02
3	.22	.11	.06	.26	.14	.07
4	.37	.20	.10	.41	.22	.12
5	.50	.28	.15	.53	.30	.16
6	.60	.35	.19	.62	.37	.20

birds older than b that bred, we used the formula $p_{adb} = p_{bb}/(1\text{-}p_y)$ where p_{adb} = proportion of adults (birds older than b) that bred; p_{bb} = the proportion of all birds that bred; and p_y = the proportion of birds younger than b (as determined from Table 2).

Per cent of adults breeding

Many investigators have divided the non-breeding population into birds which did not gain a territory and ones which did, but then did not breed. This distinction can be accommodated by expressing per cent of adults breeding as per cent of adults gaining a territory times per cent of territorial adults that breed.

Studies reporting the per cent of birds breeding were presented at the Symposium (or previously) for every swan species except Coscoroba (Table 3). Perhaps the most striking fact revealed in the summary of these estimates is that in most studies <40% of the birds four years and older breed in an average year, and this generalization appears to hold for every species. As noted above, this conclusion rests on the assumption that all breeding is done by birds more than 4.0 years old. If some birds younger than 4.0 breed, then the proportion of birds older than 4.0 breeding is even lower than reported in Table 3. It might also be argued that in some populations, few birds breed until their fifth year. Calculations similar to those reported in Table 3 (in parentheses) indicate, however, that even if all breeding is done by birds older than 5.0 years, it is still true that <50% of these birds breed in an average year in most populations.

Scherner (pers. comm.) presents evidence that Mute Swans in NW Germany that breed one year have a probability of breeding the next year of only 50-70%. This low rate of nesting again, in combination with delayed first breeding, might explain the low rates in Table 3. Beekman (pers. comm.), however, believes that virtually all birds in the Mute Swan population he studies breed every year once they have bred a first time. This entire issue needs more careful analysis. We know of few other avian groups in which so many adult-aged birds holding territories fail to breed.

Another trend evident in Table 3 is that the more northerly-breeding birds tend to have good success getting a territory but are rather unlikely to breed on it, whereas birds breeding in more

Table 3. Proportions of swans gaining territories and breeding (laying ± egg). Percentages for birds ≥4.0 years old (rather than for all birds) are given in parenthesis.

Species	Location	% of birds with territories	% of Terr'l birds that breed	% of birds that breed	References
Bewick's	NE USSR	—	—	23 (29)	Kondratiev
Swan	NW USSR	88 (100)	25	22 (28)	Mineyev
Tundra	N Alaska	77 (96)	44	34 (43)	Bart *et al.*
Swan	W Alaska	50 (63)	39	20 (25)	Dau (1981)
Whooper	Iceland	40 (51)	33	13 (17)	Rees (pers comm.)
Swan	Finland	—	—	30 (38)	Haapanen (pers. comm.)
	NE USSR	—	—	20 (26)	Kondratiev
Trumpeter	Montana	33 (42)	90	30 (38)	Mitchell (pers comm.)
Swan	Alaska	30 (38)	67	20 (25)	King (pers. comm.)
Mute Swan	Britain	34 (43)	72	24 (38)	Sears (pers. comm.)
	Scotland	40 (50)	90	36 (37)	Coleman (pers comm.)
Black Swan	N Zealand	—	—	22 (31)	Williams (1981)
B-n'd Swan	Chile	—	—	14	Schlatter *et al.*

favourable climates often fail to find a territory but generally breed if they do get a territory. For example, compare Bewick's Swans and Tundra Swans breeding in northern Alaska, with Trumpeter Swans breeding in Montana and Mute Swans. Whooper Swans, Tundra Swans in western Alaska, and Trumpeter Swans in (central and southern) Alaska breed at intermediate latitudes and show intermediate patterns. It is tempting to conclude that the populations breeding in the harsh, far-northern climates encounter conditions that frequently depress their populations and prevent density dependent regulation from becoming important. Thus, they are usually able to obtain territories, but having done so, often find conditions too poor to permit breeding. In more favourable climates, the situation is reversed. Territories are in short supply but once obtained usually contain sufficient resources to permit breeding.

Another, less interesting, possibility, is that the differences in estimates arise more from differences in survey methods. In the south, most surveys are made on the ground, and investigators have ample opportunity to judge whether birds are truly defending territories. In the north, most surveys are made by airplane, and birds occurring in pairs are usually assumed to be holding territories. If this assumption is frequently incorrect, then these errors alone could cause the differences illustrated in Table 3. To distinguish between these hypotheses we need better estimates from northern regions of how often paired birds do not claim territories, and we need similar estimates from several more localities.

Clutch size and early survival

Estimates of average clutch size and survival from laying to fledging are presented in Table 4. One immediate conclusion is that much more information from the breeding season would be valuable. In addition to the rates reported above, we tallied proportion of breeders hatching at least one egg and fledging at least one young but too few estimates were available for any patterns to emerge. The same was true of young/adult ratios in late summer and in winter. This lack of information is unfortunate because it precludes estimating survival rates during the first migration.

A few suggestions, however, can be deduced from the data in Table 4. Species breeding at

Table 4. Clutch size and early survival rates.

			Survival %			
Species	Location	Average clutch	Laying to hatch	Hatch to fledge	Laying to fledge	Reference
Bewick's Swan	NW USSR	3.1	—	—	—	Mineyev
	NE USSR	3.8	—	—	82	Kondratiev
Tundra Swan	N Alaska	3.5	—	—	—	Bart
	W Alaska	4.3	—	—	—	Dau (1981)
Whooper Swan	Iceland	3.8-4.7	—	—	—	Rees
	Finland	4.4	74	90	59	Haapanen
Trumpeter Swan	Alaska	5.4	46	48	22	King (pers. comm.)
	Montana	4.7	—	—	—	Mitchell (pers. comm.)
	Wyoming	—	—	64	—	Lockman (pers. comm.)
Mute Swan	Oxford	6.8	54	63	34	Sears (pers. comm.)
	Stafford	—	—	77	—	Coleman (pers. comm.)
	Scotland	—	—	75	—	Brown (pers. comm.)
	Rhode Island	6.2	—	—	—	Allin (pers. comm.)
	Denmark-terr	5.6	82	54	45	Andersen-Harild (1978)
	Denmark-col	5.2	58	37	21	Andersen-Harild (1978)
	Caspian Sea	6.0	79	87	69	Krivonosov
	Poland	6.0	—	—	50	Czapulak & Wieloch
	Ireland	6.7	63	64	40	Collins
Black Swan	N. Zealand	5.0	—	52	—	Williams (1981)
	Australia	4.7	55	5	3	Braithwaite (1982)
B-n'd Swan	Chile	2-5	—	10-90	—	Schlatter *et al.*

Table 5. Estimates of demographic parameters for swans. "Adult" means birds more than 4.0 years old.

Species	% of adults breeding	(Average clutch size)/2	Survival top age 4.0	Adult survival rate/yr	Location of breeding grounds
Bewick's	34	1.8	0.16	0.90	USSR
Tundra	43	1.8	0.13	0.90	N. Alaska
Whooper	38	2.2	0.14	0.88	Finland
Trumpeter	40	2.4	0.12	0.89	Montana
Mute	38	3.4	0.14	0.81	Britain
Black	31	2.5	0.19	0.85	New Zealand

lower latitudes (or in warmer areas) tend to have larger clutch sizes. Thus, the most northern species, Bewick's and Tundra, have the smallest clutch size, and Mute Swans have the largest clutch. The other swans breed at intermediate latitudes and have intermediate clutch sizes. The same pattern is shown within species by Tundra Swans and Black Swans though not by Trumpeter Swans.

This tendency for clutch size to be larger at lower latitude is of interest because in most groups of birds clutch size tends to decrease as one moves toward the equator (Gill 1989). With swans, there is some suggestion that the reverse tendency is a consequence of generally harsher conditions. Whooper Swans in Iceland had smaller clutch sizes in the colder, upland areas than in lowland areas (Rees). In Finland, pairs that had to move their young laid smaller clutches than pairs which remained on territories (Haapanen). When habitat deteriorated, both Black-necked Swans (Schlatter *et al.*) and Black Swans (Williams 1981) responded with a pronounced reduction in clutch size. In general, however, we know too little about how food quality varies in different habitats and climates. It will be interesting to investigate this issue in more detail and especially to compare swans with other birds.

Overall survival from laying to fledging varies widely. Most of the estimates are based on small samples in only a few years, however, so detailed analysis of demographic patterns during this period will have to await more data.

Survival to the end of age three

As noted in the introduction, we calculated survival from laying to the end of the third year of life by using the other rates and assuming that the population was stable. We used this approach because survivorship during this entire period is so difficult to estimate (as discussed above). Investigators preferring to estimate these rates independently might wish to determine whether, according to the rates, the population should be approximately stable. This can be done either using the simple methods we employed or, if adult survival rates vary, by using Leslie matrix methods (Leslie 1945). Many published studies - if taken literally - would suggest that the population was increasing or decreasing at unrealistic rates.

Populations with complete demographic schedules

The demographic schedules for those populations with complete data are shown in Table 5. The most striking fact about the table is the extreme uniformity of the estimates. Despite the differences between populations and species discussed above, swans appear to show great uniformity in these rates. Apparently, the basic life history approach of swans is influenced relatively little by drastic environmental changes. It would be interesting to compare this low level of variation in demographic parameters with the variation shown by other taxa that are widely distributed.

Although sample sizes are small, it seemed worthwhile to investigate relationships between the demographic rates. In general, one expects a small-to-moderate negative correlation between any pair of rates simply because as any one rate increases, some combination of the remaining rates must decline in a stable popula-

Table 6. Correlation coefficients bewtween demographic parameters for swans (see Table 5).

Variable	(Ave. clutch size)/2	Survival to age 4.0	Adult survival rate/yr
% of adults breeding	0.04	-0.85*	0.08
(Ave. clutch size)/2	—	0.01	-0.95**
Survival to age 4.00	—	—	-0.26

*p < 0.05; **p < 0.01

tion. The six possible bivariate correlations (Table 6) tended either to be close to zero, suggesting that the rates fluctuate independently of each other, or they were quite close to ±1 indicating the possibility of a trade-off between maximizing success in the two stages. In general, populations with more adults breeding had the lowest survival rates from laying to age 4.0, and populations with the largest clutch size had the lowest adult survival rate. These first indications of trade-offs in life history tactics are tantalizing, but are based on too few populations at present. We shall therefore not attempt an interpretation, while urging that more data sets like those in Table 5 will be of the greatest interest.

Suggestions for future work

As mentioned above, great benefit would result from identifying populations which have little interchange of individuals with each other. The task really involves two stages: delineation of the population, which can be done at whatever time is most convenient, and discovery of the limits of the population at all times of year. For migratory species, we suspect that delineation of the populations should be done on the wintering grounds because effective coverage for surveying and marking birds is so difficult on the breeding grounds. If a consensus among swan researchers could be developed about the identity of distinct populations, then marking and resighting on breeding, migration, and wintering grounds could be a highly effective means for learning more about swan demography and about other aspects of swan biology and conservation.

We occasionally had difficulty, in published studies, determining the exact meaning of statements about reproductive success on the breeding grounds. For example it was not always clear whether "successful breeder" meant a pair hatching one egg or fledging one cygnet. The period to which "survival" referred was also sometimes difficult to identify. Finally, in several cases, we suspect that investigators have more information than has thus far been made available for review. We hope to develop a standardized approach for reporting demographic data, and would like to correspond with other researchers interested in this effort or who have additional demographic data that we could use in our ongoing effort to summarize what is known of swan demography.

Many areas in swan research seem likely to produce substantial progress in the near future. We would like to mention three specifically. First, the low apparent breeding rate of adults is puzzling and, if verified, deserves additional study. It would be especially interesting to determine how many of the non-breeding, adult-aged birds have not bred previously, and to determine whether birds that breed one year are more or less likely to breed the following year. Second, the effect of habitat and breeding site latitude on the general life history strategy should be a fruitful area for additional work. This review shows that populations breeding at the highest latitudes have high survival rates which are attained at an early age, and have reduced clutch sizes, compared to populations breeding at lower latitudes. Several hypotheses to explain the proximate and ultimate cause of this pattern could be investigated. The relationship between habitat, breeding latitude and other aspects of the life history pattern such as age at first breeding and degree of parental care might also be studied. The third area likely to produce interesting insights is comparison of swans with other taxa. The finding that trends in clutch size for swans are opposite to those observed in many other species is one example. Many others can be imagined.

In conclusion, it seems worth noting, as did the previous article, that opportunities for international collaboration among swan biologists have never been more promising nor have they had greater potential for increasing our understanding of swans and the natural world in general. It may be hoped, therefore, that the Fourth International Swan Symposium, which will be held in Odessa, USSR, in 1994, will include a dramatic increase in the number of papers jointly authored by biologists from different countries.

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