ARE CORMORANTS *Phalacrocorax carbo* WINTERING IN SWITZERLAND APPROACHING CARRYING CAPACITY? AN ANALYSIS OF INCREASE PATTERNS AND HABITAT CHOICE

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ABSTRACT The increase rate of Cormorant numbers overwintering in Switzerland between 1970 and 1990 was the same as in the strongly growing breeding population. From 1930 to 1970, however, wintering Cormorants increased while the breeding population remained stable. The reasons are believed to be a better food supply as cyprinid and percid fish biomass increased due to eutrophication of Swiss lakes. Conversely, the increase rate of overwintering birds in Switzerland recently began to slow down while numbers during autumn passage are still following the growth of the breeding population. The resulting sigmoid pattern suggests that Cormorant numbers in Switzerland in winter are approaching carrying capacity. Cormorant density on lakes is strongly correlated with density of Perch and cyprinid fish, especially Roach, which shows signs of decrease as the input rate of nutrients into lakes is being reduced. The stepwise process of filling up different types of water bodies partly supports the Fretwell-Lucas model of habitat occupancy although behavioural responses to reduced persecution may also be involved in habitat choice. Even if increased winter survival were partly responsible for the current strong population increase (which is in fact unknown), the inland waters of western and central Europe hold a too small part of the north-central European Cormorant population (estimated at 300 000 birds in spring 1992) compared to coastal areas, as to play an important role in such a process.

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INTRODUCTION

The group of seabird species that increased markedly in numbers and expanded their breeding areas during the last 100 years, such as Northern Fulmar *Fulmarus glacialis*, Northern Gannet *Sula bassana*, or Herring Gull *Larus argentatus* (Nelson 1980), has recently been joined by two cormorant species: the Double-crested Cormorant *Phalacrocorax auritus* (Vermeer & Rankin 1984, Hobson *et al.* 1989) in North America and the Great Cormorant *P. carbo* in Europe (Suter 1989, Van Eerden & Gregersen 1995, Lindell *et al.* 1995). A number of reasons responsible for the population changes were identified or hypothesised, which may work alone or in combination, e.g. reduced exploitation, persecution and harrassment by humans in breeding colonies, reduced contamination by organochlorine contaminants, behavioural and genetic changes, and improved feeding conditions due to habitat alterations, water eutrophication and fishery practices. Most of these factors affect the production of offspring but have also allowed expansion into new breeding areas. Little is known about effects in non-breeding areas although it seems likely that the same factors may exert some influence on mortality rates. Cormorants do not breed in Switzerland, but substantial numbers use its lakes and rivers as staging and wintering areas. They have increased in a manner similar to the breeding population, but there are now signs of saturation. The objective of this paper is to analyse patterns of increase, habitat choice and habitat shifts in Switzerland compared to the evolution of breeding populations. The hypothesis that winter numbers are near carrying capacity will be considered in the light of theory of habitat occupancy, developed by Fretwell & Lucas (1969) and modified since (Wiens 1989).

METHODS

Winter counts

Cormorant numbers from 1967 onwards are based on the International Waterfowl Census in mid-January, except where seasonal occurrence is addressed. Nevertheless, Lake Constance is the only major lake where all counts were made during the daytime waterfowl census. At all other major and most minor sites, Cormorants were counted at the roosts shortly before dusk (details in Suter 1989). Lake Constance and Lake Geneva were completely covered and their numbers included in the Swiss total. The pre-1967 data for Lake Neuchâtel were extracted by W. Thönen (*in litt.*) from a number of mostly unpublished sources.

Breeding population

The population considered and referred to as north-central European is the breeding population of The Netherlands, Germany, Denmark, Sweden, and Poland. Population size is given either as number of breeding pairs (Fig. 2) or as number of breeding birds (all other figures and analyses), which is equivalent to twice the number of nests or breeding pairs, according to source. Figures for breeding numbers were taken from Van Eerden & Gregersen (1995) for The Netherlands, western Germany and Denmark and from Lindell *et al.* (1995) for eastern Germany, Sweden and Poland. Supplementary information is from M. Zijlstra (*in litt.*, for The Netherlands), J. Gregersen (*in litt.*, for Denmark), Jonsson (1979), Risberg (1990) and L. Lindell (*in litt.*, for Sweden), T. Menke, H. Heckenroth and E. Bezzel (*in litt.*, for the former West Germany), Zimmerman (1986) and H. Zimmerman (*in litt.*, for the former East Germany), Przybysz (1991) and J. Przybysz (*in litt.*, for Poland).

Fish yield data are taken from the biannual reports published by the Swiss Federal Fishery Agency; for the rating of the trophic status of larger lakes see Suter (1994).

Statistics

All tests are two-tailed. Slopes are compared with a t-test (Zar 1984).

RESULTS

Swiss winter numbers

Evolution of numbers Cormorants have never nested in Switzerland in historical times, but were already known as scarce passage migrants in the 16th century (Gessner 1557). Sources of the early 19th century indicate a similar status (Necker 1823, Schinz 1837). At the beginning of the 20th century, the number of records per year started to increase: 0-4 until 1910, 2-13 between 1911 and 1930, and 23-33 between 1931 and 1937 (Knopfli 1937). At the same time, small groups began to winter on four of the five large (> 80 km^2) lakes north of the Alps (Constance, Zürich, Neuchâtel, Geneva, further referred to as the "four large lakes"). Up to the mid-1960s, Cormorant numbers increased to 80-120 on each of these lakes. All other waters were visited only on passage until the late 1970s. Between 1967 and 1992, the Swiss mid-winter total strongly increased by following closely a logistic growth model where

$$N_i = 500 + \frac{8300}{1 + e^{7.87 - 0.419t}}$$

when t is set at 0 for i = 1967 ($r = 0.996$, $p < 0.001$). This model predicts an upper limit of 8800 Cormorants to be reached towards the year 2000, or 9400 Cormorants if the value for 1991 is considered a temporary setback and excluded

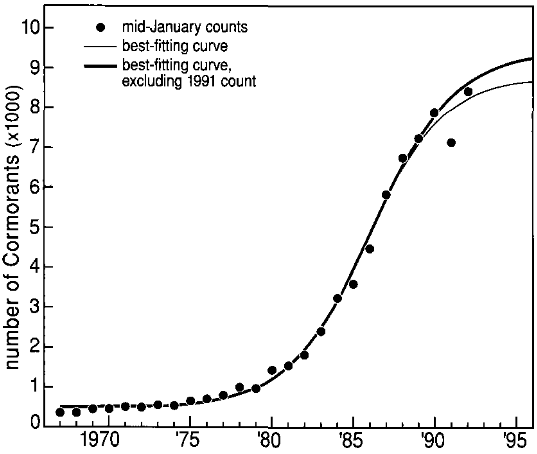

Fig. 1. Evolution of Cormorant mid-winter numbers in Switzerland, fitted with a logistic growth model.

from the calculation (Fig. 1). Two alternative models assuming unlimited growth were also tested. Although both power and exponential functions yielded only slightly lower correlation coefficients ($r = 0.986$ and $r = 0.977$, respectively), the forms of their curve were inferior to the logistic model, as shown by high autocorrelations of the residuals (logistic: $r = 0.079$, n.s.; power: $r = 0.626$, $p < 0.001$; exponential: $r = 0.715$, $p < 0.001$).

Comparison with breeding population The Cormorants migrating to Switzerland originate from the breeding population in the triangle between The Netherlands, Sweden and Poland (Reymond & Zuchuat 1995). This population remained rather stable between 1925 and the late 1970s (apart from some short-term recovery during and just after the Second World War; Fig. 2). By contrast, Swiss winter numbers steadily increased from 1930 onwards when the habit to winter on the "four large lakes" was established. The trend illustrated for Lake Neuchâtel (Fig. 2) was similar on the other three lakes (e.g. Géroudet 1987). This was apparently due to ecological changes in the lakes that made them suitable for overwintering. Water eutrophication increased productivity, which is reflected by the increased commercial yield of Perch *Perca fluviatilis* and cyprinid fish, notably Roach *Rutilus rutilus*. Cormorant numbers and Roach yield on Lake Neuchâtel (Fig. 2) were closely correlated ($r = 0.94$, $p < 0.001$), especially before 1975. There was a similar trend in Perch and cyprinid fish landings at the other three lakes, and it is generally accepted that the increased yields reflect not just a higher degree of exploitation (e.g. by the use of better gear and improved marketing facilities) but an increased fish biomass available in the lakes (Roth 1969, Laurent 1972, Nümann 1972, Hartmann 1977, Müller 1990).

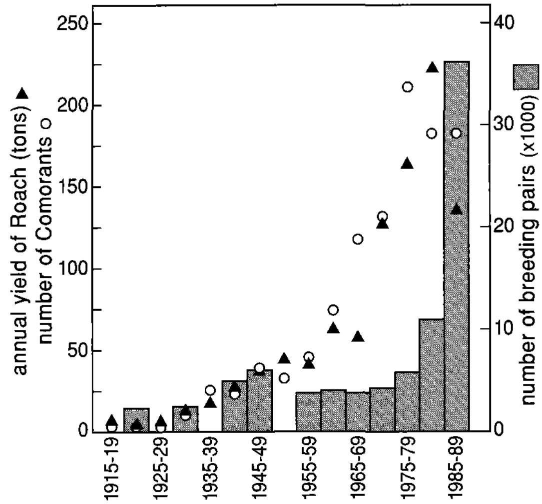

Fig. 2. Evolution of the North-Central European breeding population of the Cormorant, and 5-year means of numbers of Cormorants (mid-winter maxima) on Lake Neuchâtel compared to the yield of Roach at Lake Neuchâtel.

After 1975 breeding populations in north-central Europe started to increase rapidly, and Swiss winter numbers now followed closely the population growth of the breeding areas (Figs 3, 4). There was no difference in the increase rate in the period 1978-1991 for log-transformed values between Switzerland and eastern Germany ($t = 1.59$, $p > 0.05$) or Poland ($t = 0.15$, $p > 0.5$), and neither between Switzerland and the combined populations of The Netherlands and Denmark

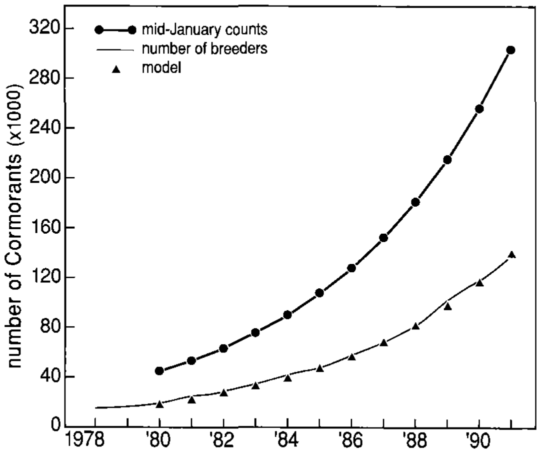

Fig. 3. Evolution of numbers of breeding Cormorants in North-Central Europe, and numbers during mid-winter in Switzerland in the subsequent year ($x = x_{i+1}$).

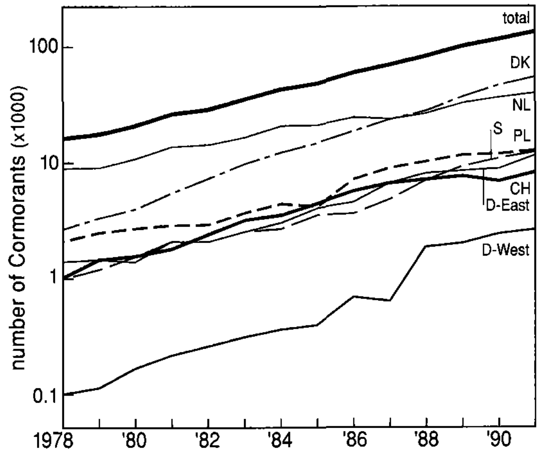

Fig. 4. Evolution of numbers of breeding Cormorants in north-central Europe (counted and modelled population) and size of total population by the end of the subsequent winter ($x = x_{i+1}$) calculated from the model population.

(t = 0.36, $p > 0.5$), or Sweden, Germany and Poland (t = 1.46, $p > 0.1$), or the total breeding population ($t = 0.23, p > 0.5$). The increase rate in Switzerland was smaller than in western Germany (t = 11.47, $p < 0.001$), Denmark (t = 12.60, $p < 0.001$) and Sweden (t = 4.24, $p < 0.001$), but higher than in The Netherlands (t = 8.76, $p < 0.001$). Since 1988, however, it was slower than in the breeding countries. Swiss winter numbers grew from 1988 to 1992 by 24%, while the increment in the breeding areas between 1987 and 1991 was 49% and ranged from 37% in Poland to 342% in western Germany. It was 67% in The Netherlands and 138% in Denmark, the two countries that provide most of the Cormorants wintering in Switzerland (Reymond & Zuchuat 1995).

To calculate the size of the late winter population, and the percentage wintering in Switzerland, I developed a simple model (Fig. 4) using the numbers of breeders between 1978 and 1980 in the north-central European population. Its assumptions are: (1) recruitment: all Cormorants start breeding at the end of the 3rd year and (2) mean number of fledged chicks per pair is 1.7 (Van Eerden *et al.* 1991, Gregersen 1991), (3) mortality rates are 30% in the first year, 20% in the second, 14% in the third, and 9% in older birds (values after Kortlandt 1942, reduced). Although the model does not account for yearly fluctuations, it follows the observed trend closely (Fig. 4). Assuming further that mortality occurs mainly between the end of the breeding season and late winter, the total size of the Cormorant population in late winter would be 2.1 times the number of breeders in the previous year. For 1991-92, it is calculated at 300 000 Cormorants. The percentage counted in Switzerland increased from 3.4 to 4.5% between 1982 and 1988, but dropped to 2.8% in 1991 and 1992.

Mid-winter numbers and seasonal peak numbers Until around 1982, highest numbers were present in Switzerland by mid-winter, indicating that Cormorants were predominantly winter visitors. With breeding populations strongly growing, seasonal peaks shifted to the period of late October - early December at most major sites (Suter 1989). By contrast, places colonized only recently (e.g. rivers), may still show the peak in mid-winter. Numbers of passage migrants therefore increased at higher rates than

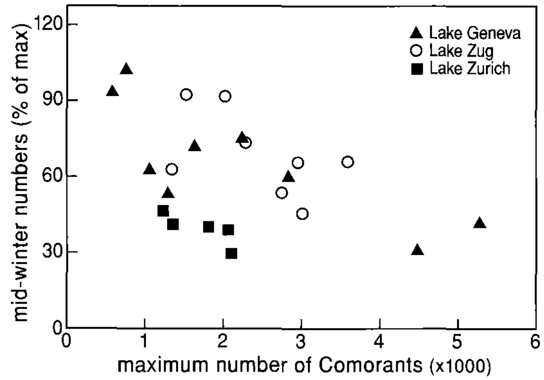

Fig. 5. Mid-winter numbers of Cormorants in Switzerland expressed as percentages of autumn peak counts, plotted against numbers in autumn peak (for years between 1982-83 and 1991-92 where autumn data are available).

numbers of overwintering birds. The discrepancy is most pronounced at lakes with a relatively high Cormorant density but less at lakes with comparatively low numbers, where local ecological effects may be more important (e.g. Lake Constance, Lake Neuchâtel). However, the fact that the difference becomes larger with increasing numbers on passage (Fig. 5) suggests that the short-term autumn peaks are still determined by the growing population size, whereas winter numbers appear to be limited by local conditions.

Habitat choice

Shifts between habitat types Until 1977, the "four large lakes" were the only waters to hold overwintering Cormorants. These are mesotrophic to eutrophic lowland lakes with a surface between 90 and 580 km^2. The only other lake of this size category (Lake Lucerne), an oligotrophic to mesotrophic pre-alpine lake, had practically no Cormorants until 1986. From 1978 onwards, the comparatively small (38 km^2) but highly eutrophic Lake Zug was colonised, and thereafter most other lowland lakes, river dams and also many free-running stretches of larger rivers (Fig. 6). The process was stepwise and characterised by a sudden colonisation of various sites followed by a rapid build-up of numbers. Similar to the Swiss total, increase patterns in the four habitat types (Fig. 6) are *s*-shaped. Some irregularities in 1985 and 1987 (cold January) that seem to be complementary between the groups may be attributable to emigration from partly frozen lakes. Increase rates since 1978-80 were highest at the two groups of predominantly smaller and highly eutrophicated lakes (Lake Zug, "other lakes"), intermediate at rivers and smallest at the "four large lakes". At the smaller lakes, upper asymptotes were reached within 5-7 years. At the "four large lakes" and on the rivers Cormorant numbers are only now tapering off. However, predictions are difficult for these two categories as they both contain sites with large fluctuations that have

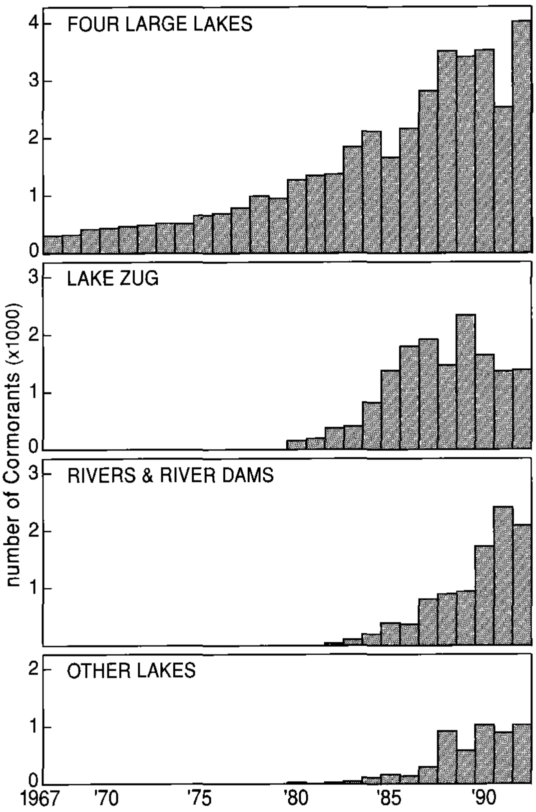

Fig. 6. Numbers of Cormorants in Switzerland, January 1967-1992, on different types of water bodies.

produced most of the group variation (Lake Geneva, Klingnau Dam).

The proportion of Cormorants staying at rivers increased from 10% in 1985 to 33% in 1991 and dropped to 25% in 1992. These figures refer to birds counted at roosts, but a number of Cormorants roosting at lakes visits rivers for foraging regularly in mid-winter (only few vice versa). With the information from the daytime waterfowl census, the percentage of Cormorants feeding on rivers can be estimated at *c.* 39% in 1991 and *c.* 28% in 1992. However, as ecological conditions and hence diet choice on dammed rivers are more similar to lakes than to free-running river stretches (W. Suter in prep.), further differentiation is needed. The extent of feeding areas around the riverine roosts is sufficiently well known (Suter 1989, 1991a), but the relative usage of river sites for foraging can only be estimated approximately from the 1991 and 1992 waterfowl censuses at 20-40% for free-running stretches and 60-80% for dams. The figures for the Swiss mid-winter distribution of feeding Cormorants therefore are in the order of 61-73% on lakes, 19-23% on river dams, and 6-16% on free-running rivers. Although no further increase in total numbers occurred since 1989-90 apart from Lake Geneva, the trend to exploit increasingly small habitats has not yet come to a halt. In the rather mild winters 1990-91 and 1991-92, daytime visits by Cormorants were recorded regularly on most small lowland lakes of 10-100 ha surface area. Even ponds and gravel pits with < 1 ha of open water can now attract single birds or small groups. Likewise, rivers, canals and streams down to 5-6 m width and 0.5 m depth may be utilised, even if they are lined by trees.

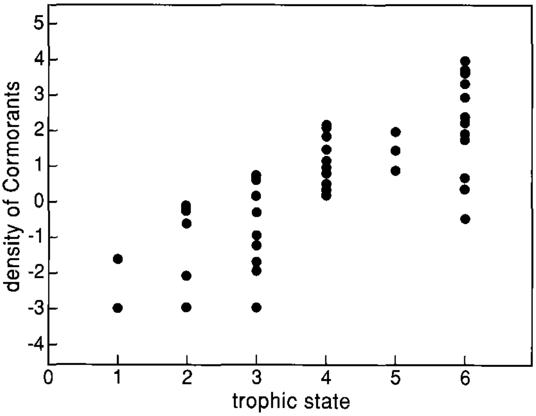

Fig. 7. Density of Cormorants (ln of numbers per km^2) at 18 Swiss lakes (> 5 km^2) during mid-winter counts in 1988-1990, and trophic category of the lakes (1 = oligo-, 3 = meso-, 5 = eu-, 6 = hypertrophic). Zero densities were assigned the value -3.

Lake type preferences The larger lowland lakes (> 5 km^2) north of the Alps still provide feeding habitat for some 70% of the winter population, yet between them, Cormorant density varies greatly from < 0.01/km^2 to 50/km^2 in mid-winter. Temporary maxima in late autumn may be around 200-300 Cormorants/km^2 on certain smaller lakes (5-10 km^2), while on a lake of 3.3 km^2 up to 1450 Cormorants were recorded (440 Cormorants/km^2). Cormorant density in mid-winter correlates positively with the trophic state of the lake (r_s = 0.806, $p < 0.001$, corrected for ties), being lowest on oligotrophic and highest on extremely eutrophic (hypertrophic) lakes (Fig. 7). Since trophic status is a measure for productivity, there should be a similar relationship between Cormorant density and fish biomass, at least for certain species. There are no data available relating directly to fish biomass present, but fishing yield by commercial fishermen may serve as an indication (Suter 1994). Cormorant density is positively correlated with both total fishing yield ($r = 0.597$, $p < 0.0001$) and the yield of cyprinid fish, mainly Roach, plus Perch ($r = 0.537$, $p = 0.0001$; Fig. 8A), but not with the yield of Whitefish *Coregonus* sp. (Fig. 8B). These correlations are based on ln-transformations, since absolute values vary greatly, both for Cormorant density and fishing yield. On several smaller but highly eutrophic lakes with accordingly high Cormorant density in late autumn, values were low in mid-winter when the census was made. On the other hand, cyprinid yield is low in at least two lakes despite high biomasses present, since fishermen

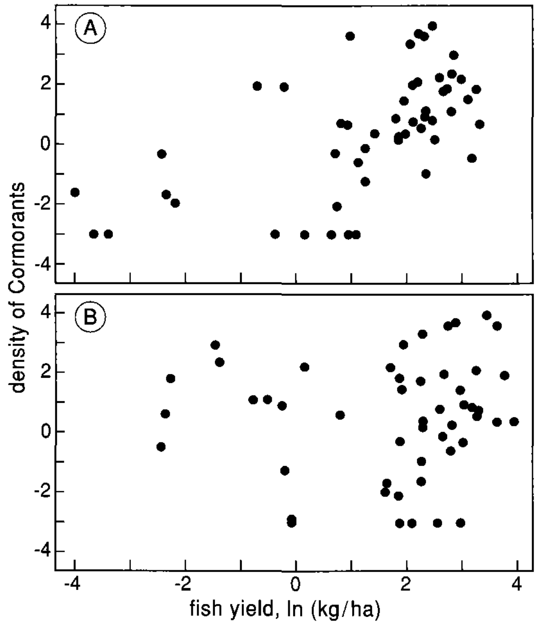

Fig. 8. Density of Cormorants at 18 Swiss lakes (as in Fig. 7) in relation to commercial yield of cyprinid fish Cyprinidae (without Bream *Abramis brama*), Perch *Perca fluviatilis* (A), and of Whitefish *Coregonus* sp. (B).

are able to select for Whitefish which are intensively stocked. Morphometric characteristics of lakes, such as shoreline types or the extent of shallow water, were not found to have a significant influence on Cormorant density (Suter 1994).

Roost sites Roost sites are usually well demarcated and separated from each other. Exceptions are Lake Constance where, besides normal roosts, groups of Cormorants use the many wooden posts set up for fishery or navigation, and some riverine roosts disturbed and scattered by anglers. Apart from such sites, there were at least 40 roosts (23 at lakes, 17 at rivers) occupied in mid-January 1992. The oldest known roost has been in use for more than 50 years at Lake Geneva (Géroudet 1987), but at least 20 roosts (11 of them at rivers) were established after 1985, and another 15-20 sites have been irregularly used since then. Most of the 40 active roosts in January 1992 were on deciduous trees (32, in two cases also on conifers), while artificial structures included electricity pylons (2), wooden posts or scaffolds (6 sites), and breakwaters (3 sites), sometimes in combination with trees. Roosting on gravel banks is not uncommon on Lake Constance during periods of low water level. Roost sites need some protection from disturbance, but only 21 roosts were on islets or otherwise surrounded by water, whereas 19 were situated at the shoreline. Although most of them were in quiet places, only 5-8 sites were without free access for people, while at 3 roosts the birds became used to people walking under the trees. One feature common to all sites is their location at the waterfront, to allow the birds unrestrained departure over the open water. On flat, tree-lined shores the more prominent trees are chosen, preferably those overhanging the water.

DISCUSSION

Is the growth of the Swiss winter population limited?

Logistic models have often been used to describe the growth of animal populations. Generally only laboratory populations of lower organisms follow the curve very closely, while species with more complicated life cycles often fluctuate heavily around the upper asymptote (Krebs 1985). There are several such examples among waterfowl species wintering in Switzerland, e.g. Shoveler *Anas clypeata*, Eider *Somateria mollissima* and Goosander *Mergus merganser* (Suter & Schifferli 1988). The Cormorant, however, follows the sigmoid pattern closely to near the upper asymptote. It is therefore safe to assume that the future development will not depart heavily from the model, and that the increase will come to a halt near the predicted limit of *c.* 9000 Cormorants, if no drastic changes in habitat quality are to interfere. Earlier calculations based on fewer data points had predicted between 10 000 and 12 000 Cormorants (Suter 1989, 1991a). The low value in 1991 may be the first indication that fluctuations around the upper asymptote are commencing.

Fitting logistic curves to population growth patterns implies that density-dependent regulation factors are expected to operate. In the case of the Dark-bellied Brent Goose *Branta b. bernicla* with an apparently sigmoid growth (Prokosch 1984, Ebbinge 1985), Summers & Underhill (1991) showed that the pattern emerged by chance through other reasons and that it could not be explained by assuming a density-dependent growth rate. The sigmoid pattern for the Swiss Cormorants is more pronounced, and it seems likely that it really emerged by approaching carrying capacity rather than by chance alone. Since the Swiss Cormorant counts do not represent a discrete population, capacity limits may be operating either in the breeding or in the wintering areas. In the first case, Swiss winter numbers would directly represent total population growth, while in the second case they would depend at least partly on local environmental conditions. An answer may be provided by comparing growth patterns and growth rates of breeding populations and Swiss winter numbers.

Have Cormorants reached the carrying capacity of the Swiss wintering sites?

During the period of rapid population growth, there was no difference between increase rates in Switzerland and the north-central European breeding population, or some subpopulations. The slopes fòr Switzerland and the combined Dutch-Danish population, from where most of the Swiss migrants originate (Reymond & Zuchuat 1995), are particularly similar. The Swiss lakes and rivers apparently had enough surplus capacity to take up a constant percentage of the growing Cormorant numbers. This may no longer be the case, because around 1988 the Swiss and the breeding population slopes began to deviate. Further support is lent to this view by the Cormorants on large lakes where numbers during autumn passage are still increasing while numbers of birds present in mid-winter are stable now.

Fretwell & Lucas (1969) had proposed that territorial breeding birds should fill habitats to carrying capacity sequentially along a gradient of decreasing habitat quality. This concept was later applied to wintering birds: Moser (1988) found that Grey Plovers *Pluvialis squatarola* filled up British estuaries sequentially. A similar pattern is apparent in the Cormorants when increase patterns are considered separately for four habitat types (Fig. 6). However, the patterns are not fully consistent with the model which proposes that a new habitat should be filled only when the preferred one has lost its comparative superiority with increasing bird density. For example, when Lake Zug and subsequently rivers and other smaller lakes were filled, Cormorant numbers continued to increase on the "four large lakes" (the "first choice"), indicating that these were not yet occupied near carrying capacity. Three assumptions of the model may not be fulfilled. Firstly, habitat quality (i.e. food density and availability) has not only been a function of Cormorant density, but has fluctuated strongly at several sites. Secondly, behavioural mechanisms (learning and tradition, site tenacity; Wiens 1989) must be important in the highly gregarious Cormorant, and may influence habitat choice. Cormorants have long been known to be wary towards man, and the exclusive use of four of the largest Swiss lakes for forty years probably was mainly a response to security requiring large open space, perhaps intensified by traditional behaviour. Many of the smaller waters colonised since 1977 had offered good feeding conditions for a long time before. I suggest that reduced persecution in the breeding areas since the 1970s (Hald-Mortensen 1986) has relaxed shyness by learning, perhaps even in conjunction with lessened genetic selection towards shy individuals (see Berthold *et al.* 1990). Average hunting pressure in non-breeding areas may also have decreased, although locally (e.g. in Switzerland) persecution and deterring of Cormorants have increased (W. Suter own obs.). Smaller lakes and narrow rivers, that leave feeding Cormorants more vulnerable than large expanses of water, now became acceptable. In this way their habitat quality would have increased as a consequence of altered Cormorant behaviour rather than changing environmental factors, and these waters might have gained a fitness potential for Cormorants comparable to the "four large lakes". Thirdly, there are sex and age related differences in winter distribution of Cormorants on a large geographical scale (Van Eerden & Munsterman 1986, Munsterman & Van Eerden 1991), and such have also been found for habitat use near breeding sites (Erlandsson *et al.* 1991). Evidence exists that Cormorant dispersion over habitat types in Switzerland is also unequal with respect to social status and experience given by sex and age (W. Suter own obs.). The Fretwell-Lucas model might consequently still be operating although it would not be detected on the basis of numbers alone. Despite the equivocal evidence for the Fretwell-Lucas model, by comparing increase patterns in the four site categories, one can nevertheless conclude that Cormorant numbers wintering in Switzerland are now approaching carrying capacity. All patterns are sigmoid, and numbers are near the upper asymptote, except possibly in the river category, which still seems to have some capacity for growth. Cormorant increase patterns in Bavaria have recently also been interpreted as approaching upper limits (Bezzel 1992).

Which parameters are important in limiting wintering Cormorant numbers?

Habitat requirements of wintering Cormorants include at least four major prerequisites: open water, food, roost sites, and security. Even in cold winters, most larger Swiss lakes do not freeze up, and many of the smaller lakes (< 20 km^2) usually also stay open, due to their depth and exposure to wind. The diminishing importance of security has already been discussed; it was also noted elsewhere (Martucci 1990). Likewise, the availability of roost sites is apparently not limiting. From 1987 to 1992, Cormorant numbers outside Lake Constance (where roost occupancy is not well known) increased from 4900 to 7300, i.e. by 50%, while the number of roosts nearly doubled from 18 to 32. Almost all of the new roosts were established in areas that had already been exploited for some time by birds roosting elsewhere. New roosts appear to have been set up to reduce travelling distance rather than to avoid crowded conditions at the old sites, which anyway are capable to accommodate up to 3-4 times more birds during autumn passage than in winter.

Food is more likely to be limiting. Cormorant density on lakes is linked to the biomass of cyprinid fish (mostly Roach) and Perch present. These species form on average more than 80% of the Cormorant diet in Switzerland, while Roach alone accounts for more than 60% (W. Suter own obs.). Percid and cyprinid fish constitute most of the diet in many north and central European freshwater habitats, and Roach is often an important component (Marteijn & Dirksen 1991, Keller 1992). It is, however, not as dominant in the food taken from shallower waters than it is in the deep Swiss lakes, where the shoaling habit of fish is crucial to their efficient utilisation (W. Suter own obs.). That Roach may play a key role for Cormorants in most Swiss lakes is further substantiated by the strong correlation of the early increase by wintering Cormorants on Lake Neuchâtel and the increase of Roach yield. On a more anecdotal level, recent cases showed that Cormorant numbers either dropped sharply (Lake Sempach) or that spatial distribution of the birds changed suddenly (Lake Zug), after large Roach shoals which had been the main food source had disappeared or become unavailable. It is not known whether Cormorants themselves are able to exert some long-term influence on Roach populations, but existing data on predation rates do not support this possibility for larger lakes (Suter 1991b, Platteeuw *et al.* 1992). However, Roach biomasses are expected to decrease, when the nutrient input into lakes which is being steadily reduced, results in decreasing primary production. The latest Roach yields indicate that biomasses are lower now in several lakes (Müller 1990). Oxygen content of deeper water layers is also improving and probably allows fish shoals to stay at greater depth in winter, thereby further reducing food availability to Cormorants.

Prospects and the importance of inland wintering

The increase of wintering Cormorants on rivers and river dams is not only a function of population size and available food, but most likely a process of behavioural adaptation is also involved. Thus, river habitats could still gain relative importance in the immediate future. Most rivers, however, are already occupied to the extent that even sections where Cormorants are able to dive only in the deeper hollows are used. It is therefore unlikely that rivers will continue much longer to provide opportunities for increasing numbers of Cormorants passing through Switzerland. Altogether, the most likely conclusion is that winter numbers in Switzerland and adjacent areas are near carrying capacity, that they will eventually fluctuate around 9000 Cormorants, and that rivers and river dams might accommodate some 40% of the winter population in the long term.

The question remains whether the availability of food-rich inland wintering habitats in central Europe may have played a role in the increase of the Cormorant population, especially in its earlier stage. There is no quantitative information on winter mortality rates, let alone regional differences in these. But because the Swiss waters hold only 2.8% of the total winter population, the percentage wintering in all inland areas in central and western Europe (in addition mainly The Netherlands, France, southern Germany and Austria) probably does not exceed 15-20%. The vast majority winters along the fringes of the Mediterranean, the Atlantic and the southern Baltic. If winter survival is suspected to have increased, cues should be sought in marine and coastal habitats where the current expansion is accommodated in winter.

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SAMENVATTING

In Zwitserland laten de aantallen overwinterende Aalscholvers tussen 1970 en 1990 vrijwel dezelfde toenemende tendens zien als die van de gecombineerde broedpopulatie van Nederland en Denemarken, waar de meeste vogels vandaan kwamen. Vóór 1970 was er in Zwitserland al sedert 1930 sprake van toenemende aantallen overwinteraars, hoewel in die periode de broedpopulatie nog vrijwel stabiel was. Als voornaamste reden hiervoor wordt aangevoerd dat het voedselaanbod in de Zwitserse meren in die periode stelselmatig beter is geworden als gevolg van eutrofiëring. Hierdoor is de stand aan met name Blankvoorn en Baars sterk toegenomen. Dit verklaart de positieve correlatie tussen eutrofiëringsgraad en aantallen Aalscholvers per meer.

In de meest recente jaren is de toename van overwinterende vogels duidelijk afgenomen, terwijl zowel de broedpopulatie als de aantallen doortrekkende vogels nog altijd een sterkere groei laten zien. Dit wordt verklaard door de veronderstelling dat de draagkracht van de meeste gebieden wordt bereikt. Bovendien begint het bestand aan vooral Blankvoorn in vele meren terug te lopen als gevolg van een vermindering van de nutriëntentoevoer.

De stapsgewijze invulling van verschillende winterbiotopen door Aalscholvers in Zwitserland volgt gedeeltelijk het model van Fretwell-Lucas. Dit model voorspelt dat habitats opgevuld worden volgens een patroon van afnemende kwaliteit. De af en toe optredende afwijkingen van het model worden vooral verklaard met de veronderstelling dat Aalscholvers in de loop der jaren als gevolg van verminderde vervolging minder schuw zijn geworden, waardoor ook kleinschaliger gebieden met een goed voedselaanbod aantrekkelijke overwinteringsgebieden zijn geworden. Tenslotte wordt vastgesteld dat - zelfs als een verbeterde overleving in de winter een bijdrage zou hebben geleverd aan de enorme populatietoename in Europa - de landinwaarst gelegen overwinteringsgebieden in Zwitserland een te gering aandeel van de totale populatie (geraamd op zo'n 300 000 vogels) herbergen om hierin enige rol van betekenis gespeeld te kunnen hebben.

ADDENDUM

Swiss mid-winter totals dropped sharply to 6500 Cormorants in 1993 and further to 5800 in 1994. Predictions bases on the form of the growth curve have therefore become more difficult, although it seems now more likely that future winter numbers will fluctuate in the region of 5000-7000 rather than stabilise at 8000-10 000 Cormorants.