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Waterbird dynamics at the shallow Lake Krankesjön, southern Sweden: a long-term study

Beståndsvariationer i Krankesjöns simfågelfauna: en långtidsstudie

HANS KÄLLANDER, LARS-ANDERS HANSSON, CHRISTER BRÖNMARK & ALICE NICOLLE

Abstract

This paper reports the within-year and between-year variations in the number of waterbirds at Lake Krankesjön, southern Sweden based on counts carried out during 1985 to 2007. The background to these counts was a dramatic decrease in the number of Great Crested Grebe *Podiceps cristatus*, Mute Swan *Cygnus olor* and Common Coot *Fulica atra* from 1974 to 1976, concurrent with a deterioration of water transparency and a nearly total disappearance of submerged vegetation. In 1985, when the regular counts of waterbirds started, the lake had just begun to recover. Numbers of moulting and staging waterbirds increased rapidly as the conditions improved. Numbers of grebes, swans and coots over the two decades correlated with limnological variables, and it is concluded that their numbers depend on the amount of submerged vegetation, in turn determined by water transparency.

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Introduction

Lake Krankesjön in southern Sweden (55°42' N, 13°28') got its reputation as a first class bird-lake through Swanberg's (1931) book on its bird fauna and, in particular, by his discovery of a colony of Black-necked Grebes *Podiceps nigricollis*, the first breeding record of the species in Sweden. The Black-necked Grebes seem to have disappeared from the lake some time during the latter part of the 1930s, but the lake's popularity among bird watchers has remained to the present day. However, in the years 1974–1976 a drastic decline in the populations of some waterbirds was recorded (Karlsson et al. 1976). Although the observations on which this conclusion was drawn were made without a spottingscope (only binoculars were used) and some of the figures therefore may be on the low side, there is no doubt that the decline in waterbird numbers was both real and dramatic. Thus, the mean number of Great Crested Grebes *Podiceps cristatus* observed in July fell from 50 in 1974 to only 3.5 in 1976; the number of Mute Swans *Cygnus olor* during July–September from a mean of 40.6 to 0.5; and those of Common Coots *Fulica atra* during the same period from c. 1000 to a single bird (calculated from Karlsson et al. 1976). That these changes were a local phenomenon is shown by data from the Swedish Waterbird Counts: the 1976 index figures for both Common Coot and Mute Swan were very high, for the Coot the highest during the period 1963–2006 (Nilsson 2007). Concurrent with the decrease in bird numbers a change occurred in the transparency of the lake's water. From having been relatively clear, the water became highly turbid, and this change seems to have taken place very rapidly. This had the effect that practically all submerged vegetation, which had been dominated by *Chara* spp., disappeared. Interestingly, the same change took place simultaneously at another shallow lake, Lake Björkesåkrasjön, 19 km to the south of Lake Krankesjön (Karlsson et al. 1976). Unfortunately, few limnological data exist for the period immediately after the drastic deterioration of the lake in the mid-1970s, but those few that exist show that the poor state of the lake remained for more than ten years (Andersson et al. 1990). Thus, in 1982 water turbidity was very high and transparency correspondingly low.

To study the relationship between bird numbers and various limnological variables, the late G. Andersson started regular counts of the lake's waterbird community in summer 1985. With two gaps, in 1997 and in 2000, these counts have continued to the present day. As will be shown below, the waterbird counts started at about the same time as the lake began to recover (also cf. Andersson et al. 1990). The aim of the present paper is to present the results of the first 21 years of the study. We first describe, for the majority of the waterbird species, their seasonal pattern of occurrence and then their population fluctuations. However, we do not treat grebes other than the Great Crested Grebe, geese, herons, rails (other than the Common Coot), gulls and terns, nor any of the various rare birds that have visited the lake only occasionally. Finally we discuss possible causes for the numerical fluctuations of the waterbird community, with an emphasis on those few species that seem to be good indicators of the limnological status of the lake.

Methods

Study area

Lake Krankesjön, 3.4 km^2 in area, is very shallow, with large parts less than a metre deep. In a restricted area, the water depth reaches 3 m, but most of the lake is much shallower and has a mean depth of c. 1.5 m. During periods with clear water about half of the lake's bottom area is covered with submerged plants, especially charophytes, which dominate the bottom vegetation of most of the lake. Smaller areas with *Potamogeton pectinatus* also occur. The lake is fringed by reeds *Phragmites australis* that form more extensive beds in the west and in the southeast. In the eastern part there are also a few small, isolated clumps of reeds as well as low, island-like stands of *Acorus calamus*, *Sparganium*, etc. Two very small streams enter the lake, one from the southwest, one from the southeast, while the outflow is towards the north. The lake is surrounded by the permanent grasslands of a military training area, so the small streams bring only small amounts of nitrogen and phosphorus from agriculture to the lake.

Bird counts

The waterbirds were counted from two bird observation towers, one on the southern shore, one in the east. During the early years, supplementary observations were sometimes also made from a gap in the vegetation on the northern shore. From summer 1985, when the monitoring of the waterbirds started, until 2003, birds were normally counted twice a month. In most years counts started in mid-April and continued until mid-October, but in some years they also included the winter months. After 2003, counts have been more frequent and have been carried out year-round. A few gaps exist in the data series. As mentioned above, no counts were carried out in 1997 and 2000, and in 2001 they did not start until July. The number of counts is given in Table 1. It is important to note that, during the last four years, not all waterbird species were counted during each visit; sometimes only the individuals of some of the more important species (e.g. Mute Swan, Common Pochard *Aythya ferina*, Common Coot) were counted or, more often, most but not all species.

Observations were made with binoculars and (mainly) with spottingscopes. With the better optics available during the last four years, observations were quite frequently made only from the eastern observation tower, from which all of the lake can be viewed. In conditions of good visibility, it is possible to find and identify birds also in the westernmost part of the lake (which usually accommodates fewer birds than the central and eastern parts). However, during counts from the eastern tower only, it is likely that a few birds have been missed sometimes, for instance single female Tufted Ducks *Aythya fuligula* and, in winter, female Smews *Mergus albellus*. Such misses, however, fall within the error margins of the counts and are totally unimportant for the main aim of the study.

Sometimes numbers for a particular species varied markedly between adjacent counts, even on a day-to-day basis. Such variation can have two causes: a turnover of individuals or counting errors. Often it was obvious that the first applied, for instance for some species of dabbling duck in autumn, when flocks sometimes were seen arriving at the lake, or leaving, during a count. In other cases counting errors seem more likely. The precision of counts of Coot depends strongly on the birds' dispersion on the lake; when Coots packed tightly together in response to the appearance of a White-tailed Eagle *Haliaeetus albicilla*, they were impossible to count altogether. Also when ice had concentrated them to small areas of open water, counting was difficult, but also in more normal conditions, the form of the flocks influenced the accuracy of the counts. For one species in particular, the Great Crested Grebe, the number detected was strongly dependent on wind speed. As soon as there was some wave action, grebes became difficult to detect. Also their diving activity and long under-water stays influenced the chances of detecting them.

To test for possible trends in the material and to look for correlations between bird numbers and year,

Table 1. Number of days per month and year that waterbirds were counted at Lake Krankesjön during 1985–2007. Note that the bi-monthly counts in 2003 have been supplemented with additional data and that, in the period 2004–2007, not all species were counted on every visit.
Antal dagar per månad och år som simfåglar räknades i Krankesjön 1985–2007. Under åren 2004–2007 räknades inte alltid samtliga arter vid varje besök. Räkningarna 2003 har kompletterats med en del räkningar utanför de ordinarie räkningarna.

	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Total
1985	-	-	-	-	-	1	1	1	3	2	1	1	10
1986	-	-	-	2	3	2	2	2	2	3	-	1	17
1987	-	-	-	2	1	2	2	2	4	4	1	1	19
1988	1	1	2	2	1	3	2	1	2	1	2	-	18
1089	1	2	1	3	2	1	2	3	2	1	2	1	21
1990	1	1	3	2	1	2	2	2	4	1	2	1	22
1991	-	-	2	2	2	2	2	1	2	2	2	-	17
1992	1	-	1	2	2	2	3	1	4	2	1	1	20
1993	1	-	1	2	1	2	3	1	2	2	-	-	15
1994	1	-	-	2	1	2	3	1	2	2	-	-	14
1995	-	-	-	2	2	1	3	2	2	2	1	-	15
1996	-	-	-	3	2	2	2	2	2	2	1	-	16
1997	-	-	-	-	-	-	-	-	-	-	-	-	0
1998	-	.	-	2	2	2	2	1	2	2	-	-	13
1999	-	-	-	1	2	3	2	2	2	1	-	-	13
2000	-	-	-	-	-	-	-	-	-	-	-	-	0
2001	-	-	-	-	-	-	1	2	2	1	1	-	7
2002	-	-	-	3	2	1	2	2	2	3	-	-	15
2003	-	-	3	9	4	3	2	2	5	3	-	-	31
2004	3	6	13	8	10	3	7	3	7	12	6	3	81
2005	3	3	6	14	9	3	4	5	7	11	4	1	70
2006	3	1	3	11	2	2	4	8	11	14	5	6	70
2007	2	4	9	10	8	2	6	8	11	16	10	6	92
Total	17	18	44	82	57	41	57	52	80	87	39	22	596

we used the non-parametric Spearman rank correlation, for correlations between bird numbers and environmental variables we used Pearson correlations. Calculations were made in SYSTAT (Wilkinson 1990); 2-tailed P-values are given throughout.

Results

The annual cycle

Here we describe the seasonal occurrence of a number of waterbird species at Lake Krankesjön, mainly in the form of a series of diagrams. For two reasons, the presentation is restricted to the years 2004 to 2007. First, and most important, in the earlier material counts are often lacking for the winter months (November to March) and, second, in most years too few counts were carried out to provide a good characterization of the birds' seasonal presence on the lake. The diagrams are intended to show the general seasonal pattern of occurrence of the species but also to reflect differences in timing and numbers between the four years. For six species, Great Crested Grebe, Great Cormorant *Phalacrocorax carbo*, Mallard *Anas platyrhynchos*, Northern Pintail *Anas acuta*, Smew and Goosander *Mergus merganser*, the four years have been combined to provide a clearer picture of their seasonal presence on the lake despite the fact that this obscures differences between years. The diagrams are accompanied by commenting texts; some species that occur in low numbers or very erratically are treated in text only.

Not all species were counted on each visit to the lake, and since zero occurrence (i.e. no individual detected) is not indicated in the diagrams, gaps can be the result of the species either not being counted or not being seen. Moreover, as pointed out above, variation in numbers between adjacent days can have different causes. Where appropriate, the reasons for such variation are mentioned in the treatment of the respective species.

In the diagrams, time of year is given as day

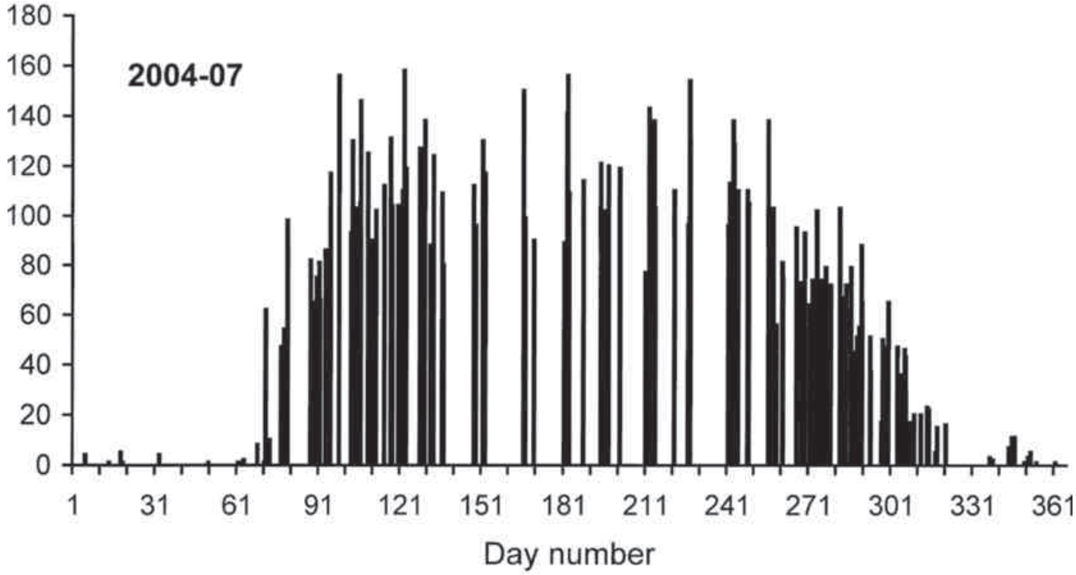

Figure 1. The seasonal occurrence of Great Crested Grebe at Lake Krankesjön. Combined data for 2004 to 2007.
Den årstidsmässiga förekomsten av skäggdopping i Krankesjön. Kombinerade data för åren 2004–2007.

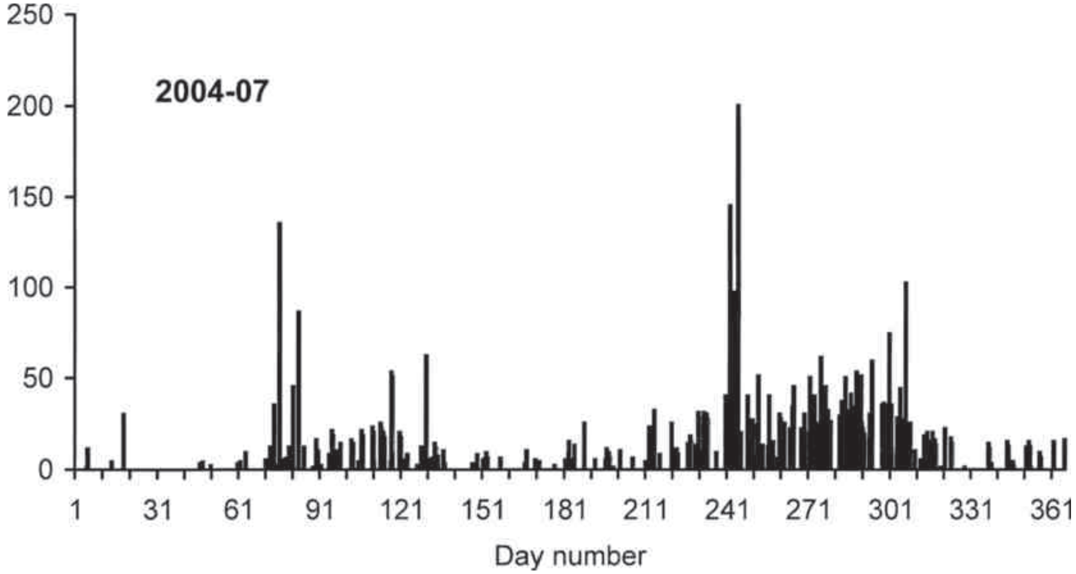

Figure 2. The seasonal occurrence of Great Cormorant at Lake Krankesjön. Combined data for 2004 to 2007.
Den årstidsmässiga förekomsten av storskarv i Krankesjön. Kombinerade data för åren 2004-07.

Great Crested Grebe Skäggdopping *(all photos: Hans Källander)*

Great Cormorant Phalacrocorax carbo

number, Day 1 = 1 January and Day 365 = 31 December. Thus, disregarding the leap-year, 1 July is Day 182. With one important exception, the scale of the Y-axes has been kept identical within (but not between) species to facilitate comparison between years. The exception is the Figure for the European Teal *Anas crecca*, in which scales differ considerably. Throughout, the Y-axis shows the number of individuals; the labelling has been omitted for technical reasons.

Great Crested Grebe *Podiceps cristatus* (Figure 1). Five Great Crested Grebes apparently wintered on the lake in 2006/07 (birds were seen in both December and January, and later in winter). Normally the species arrived at the lake when the ice broke up or, after ice-free winters, at about the same time, viz. during the first half of March. Numbers then increased rapidly. Spring 2006 was an exception in so far that the lake froze late and ice remained until the end of March. However, once the ice was gone, grebes immediately arrived, 24 grebes on 1 April and no less than 117 four days later. In all four years numbers remained high over summer, with some 130–150 birds until mid-September, after which there was a steady decrease. After mid-November very few Great Crested Grebes remained on the lake, in contrast to the situation at the much larger Lake Vombsjön (c. 12 km^2), where the number of staging grebes peaks at that time (Källander 2006). This pattern of occurrence of Great Crested Grebes seems to be typical for Lake Krankesjön and is reflected also in the material collected prior to 2004. Two additional remarks should be added. First, until August, Figure 1 is based on number of adult grebes observed. Thereafter also juveniles were included. The date this was done differed between years but, interestingly, this is not reflected in the diagrams in the form of a sudden increase in numbers. The second point is, as mentioned above, that the Great Crested Grebes are difficult to count accurately in windy conditions, even moderate winds making them difficult to detect. This is without doubt the main reason for the relatively large variation in numbers between counts, but also the level of diving activity has a strong influence on detectability (cf. Källander 2008).

Great Cormorant *Phalacrocorax carbo* (Figure 2). During 2004–2007 Cormorants were seen at the lake almost year-round, except during periods when the lake was frozen. Numbers were generally lower during spring and summer than during autumn. The highest numbers (e.g., 135 on 17 March 2004, 145 on 30 August 2004, 200 on 2 September 2004) are an effect of temporary visits by migrating flocks that landed on the lake and foraged there for a few hours before departing in a northeasterly (spring) or southwesterly direction (autumn). The large number (102) on 2 November (in 2007) is the result of counting the birds going to roost in willow trees *Salix* sp. at the mouth of the small stream that enters the lake from the southeast. Although most birds at the roost came from the lake, birds also arrived from other directions. The figure therefore includes birds that had spent the day elsewhere. Although flock-fishing cormorants are easy to detect, birds fishing alone are much more difficult to spot. For this reason, it is likely that counts during the day to some extent have underestimated the true number present. It seems fairly safe to say, however, that during the last few years some 25–30 cormorants have used the lake regularly during spring, while about 40–50 have used it during autumn.

Whooper Swan *Cygnus cygnus*. On the whole, Whooper Swans are not very common at Lake Krankesjön, but small numbers are seen in winter. There was a small peak during March, but numbers were very low (max 11 birds). At that time, migrating flocks were often seen passing the lake without landing. Birds on autumn migration started arriving in October and up to 30 individuals were recorded on a few occasions at the end of October and during the first half of November.

Mute Swan *Cygnus olor* (Figure 3). Even disregarding the long period of ice in January–March 2006, the Mute Swan's seasonal population pattern varied between the four years (Figure 3 only refers to adult, all-white birds). In 2004, winter numbers decreased gradually until early April, whereas in 2005 this decrease was abrupt. After this spring low, the pattern was roughly similar in the two years until the end of the year, however with slightly lower numbers in October–November in 2004. In 2006 numbers were generally lower than in the three other years, with only a small peak in late July–August, after which numbers, with a few exceptions, remained low until the end of the year. These low numbers then prevailed until early April 2007 despite the winter being extremely mild (compare the November–December numbers in the other three years with those in 2006). In 2007 numbers increased steadily from late October (and reached over 200 adults in early January 2008).

European Wigeon *Anas penelope* (Figure 4). As for most of the other dabbling ducks, Wigeon numbers showed two peaks, one in spring and the other in autumn. The spring peaks differed greatly in size. Thus, in 2006, when the lake did not become ice-free until the end of March, the highest spring

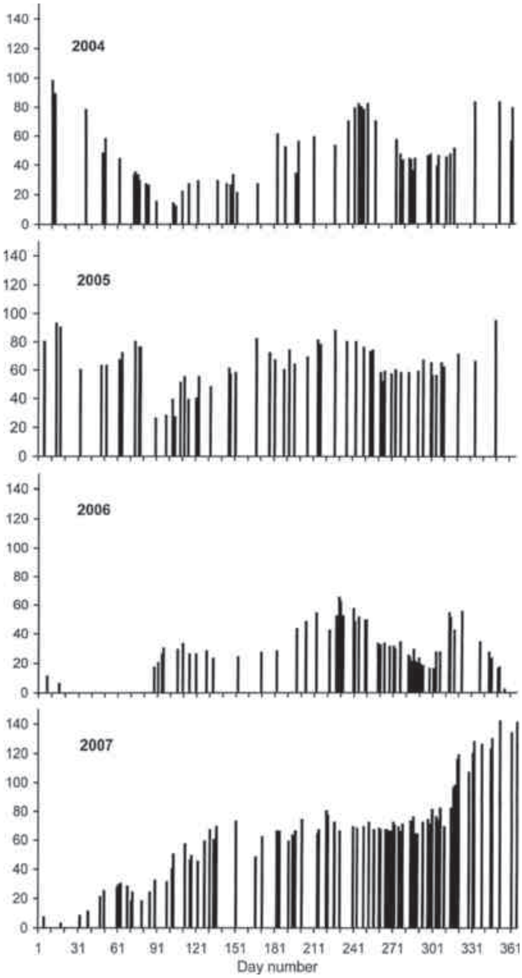

Figure 3. The seasonal occurrence of Mute Swan at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av knölsvan i Krankesjön åren 2004–2007.

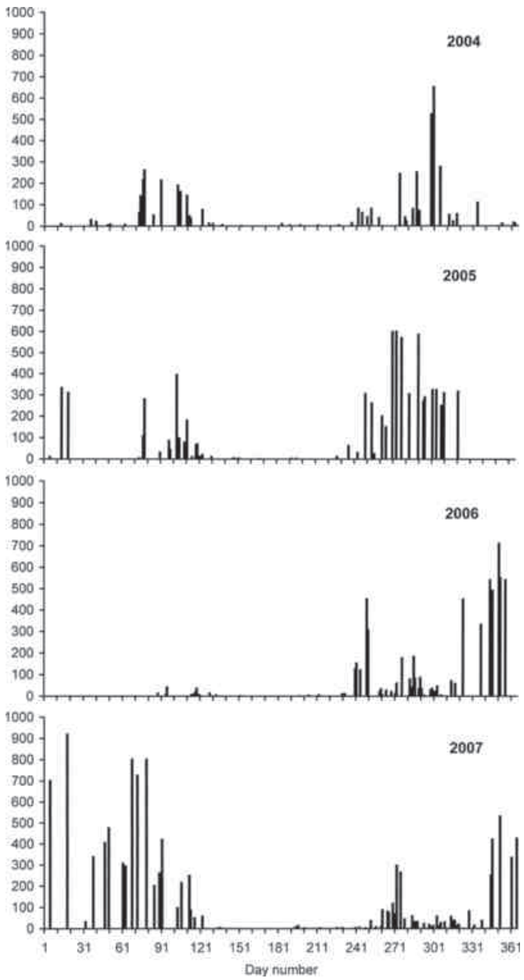

Figure 4. The seasonal occurrence of European Wigeon at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av bläsand i Krankesjön åren 2004–2007.

number recorded was only 41 birds vs 300–400 in the two preceding years. Both 2005 and 2007 were a bit exceptional (compared with those years in the period 1985–2003 from which winter data exist) in that large numbers of Wigeon were present in January (>900 in 2007). In both years the Wigeon disappeared when the lake froze, only to return as soon as the ice melted. Both this temporary absence and the influx of Wigeon in early winter in 2006 and 2007, after the normal migration period (Edelstam 1972, Ulfstrand et al. 1974), suggest that the birds arrived from near areas, such as the coast of the sound between Sweden and Denmark, where large numbers of Wigeon have recently started to winter (Nilsson 2007). During the migration period in autumn, peak numbers in both these years were only half of those in 2004 and 2005.

Mallard *Anas platyrhychos* (Figure 5). During much of the year, Mallards were difficult to count because they tended to loaf in the shelter of reed beds during the day. This was sometimes demonstrated very clearly when White-tailed Eagles vis-

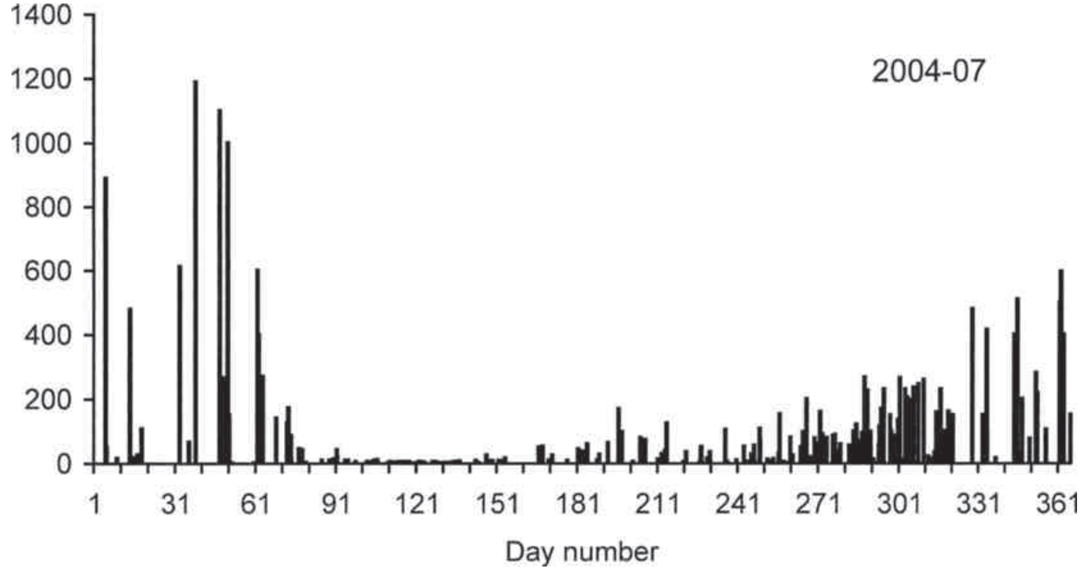

Figure 5. The seasonal occurrence of Mallard at Lake Krankesjön. Combined data for 2004 to 2007.
Den årstidsmässiga förekomsten av gräsand i Krankesjön. Kombinerade data för åren 2004–2007.

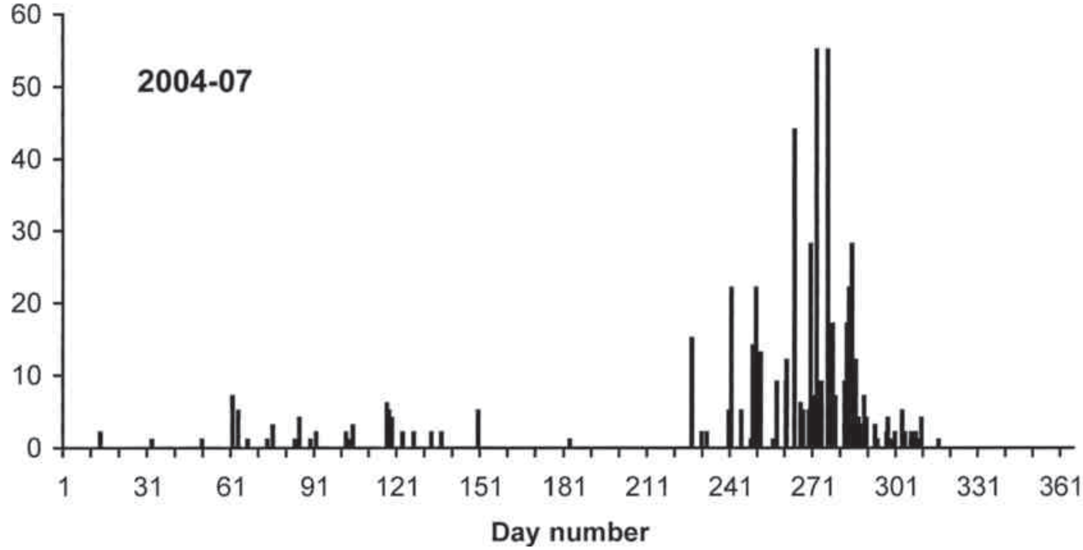

Figure 6. The seasonal occurrence of Northern Pintail at Lake Krankesjön. Combined data for 2004 to 2007.
Den årstidsmässiga förekomsten av stjärtand i Krankesjön. Kombinerade data för åren 2004–2007.

ited the lake, which in recent years they did year-round. Before the appearance of an eagle, a few tens of Mallards would have been counted; when they took flight in response to the eagle they sometimes turned out to be more than five times as many. Even so, Figure 5 gives a reasonably correct picture of the Mallard's presence at the lake. From April until June, i.e. the incubation and brood-rearing periods, very few Mallards were seen. Somewhat more birds were seen during the period of summer moult, and especially from about mid-September. The highest numbers occurred in winter, as long as at least some open water remained, a pattern also reflected in data from the earlier years of the study. The highly variable figures for January to March, both within and between years, are strongly related to the ice situation.

Northern Pintail *Anas acuta* (Figure 6). Spring numbers were always low, only once during 1985–2007 reaching 20 individuals, while autumn numbers were higher, but mostly below 50. The autumn peak fell at the end of September.

Gadwall *Anas strepera* (Figure 7). Gadwall numbers showed a fairly consistent pattern across the four years, with low numbers at least until mid-June, and a peak in the first half of September. As for the Mute Swan and Coot (see below), numbers in 2006 were lower than in the other three years.

Northern Shoveler *Anas clyepata* (Figure 8). As for the other dabbling ducks, numbers were lower in spring than in autumn, with (low) peaks in the second half of April (in 2005 the largest number was seen on 1 May). Numbers were very low in summer, but started to increase by mid-August. While the autumn peak occurred in October and November in 2004 and 2005, respectively, it was much earlier in both 2006 and 2007. Numbers also varied considerably between the four years; only in 2006 did they exceed 100 on any count.

Common Teal *Anas crecca* (Figure 9). The Teal showed a very variable pattern (notice the different scales in the diagrams), both with respect to seasonal occurrence during the four years and numbers observed. There was also considerable day-to-day variation in numbers, probably reflecting a high turnover of individuals but partly also variation in detectability. During autumn in particular, Teal, in common with Mallard, tended to loaf in shelter and only became visible after disturbance. As for Wigeon, extremely high numbers were present during the winter 2006/2007, with 2000 individuals being present by mid-January 2007.

Garganey *Anas querquedula*. The Garganey is the rarest of the dabbling ducks and was normally seen in just a few individuals mainly during April and May, with a peak around 1 May. The very few autumn observations were in August and the first half of September.

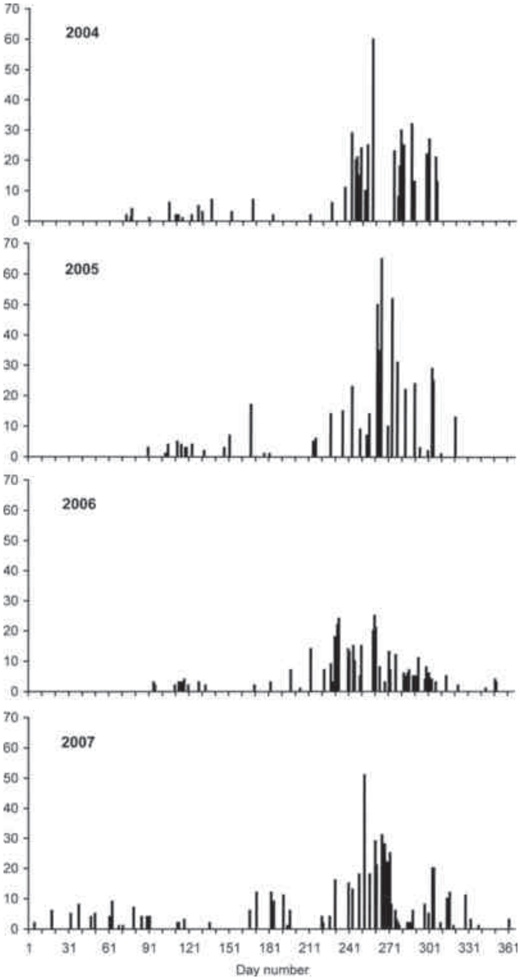

Figure 7. The seasonal occurrence of Gadwall at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av snatterand i Krankesjön åren 2004–2007.

Common Pochard *Aythya ferina* (Figure 10). Disregarding birds counted in December and January, i.e. wintering birds, the Pochard's seasonal pattern of occurrence at Lake Krankesjön was fairly consistent across the four years, albeit with some variation in numbers. Thus, numbers in autumn 2004 were higher than those in the other three years,

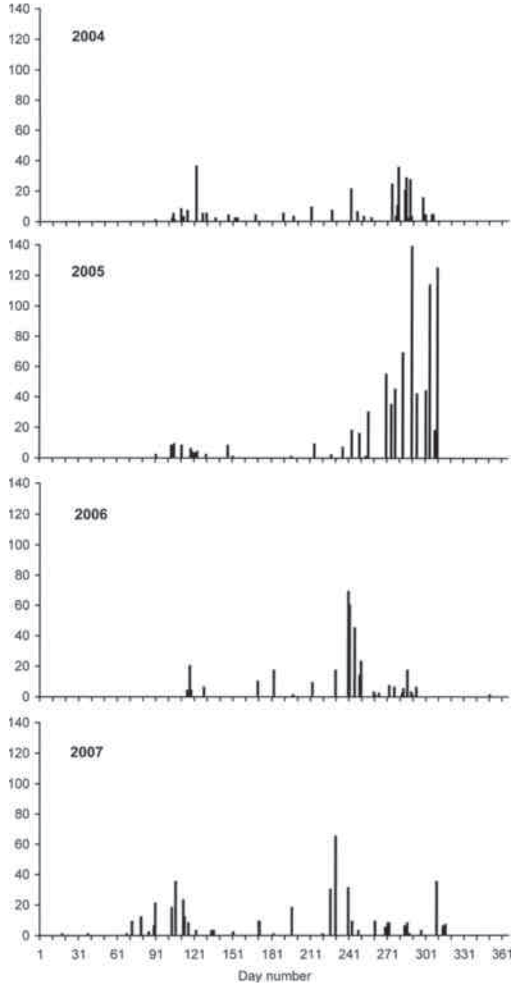

Figure 8. The seasonal occurrence of Northern Shoveler at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av skedand i Krankesjön åren 2004–2007.

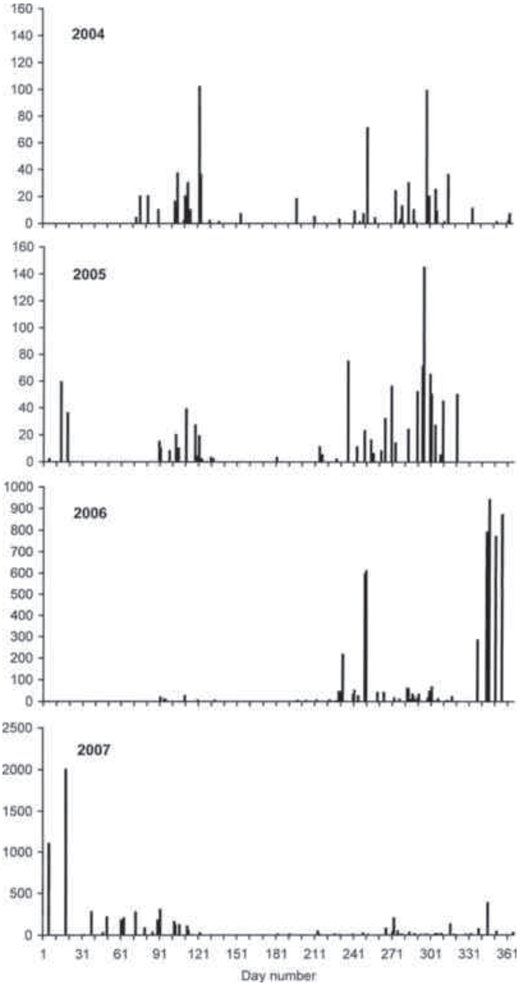

Figure 9. The seasonal occurrence of Common Teal at Lake Krankesjön in 2004 to 2007. Note the widely varying scales in the different diagrams.
Den årstidsmässiga förekomsten av kricka i Krankesjön åren 2004–2007. Observera att delfigurernas skalor skiljer sig åt markant.

while low spring numbers in 2006 may have been an effect of the late ice break-up and subsequent fast migration from the wintering areas. In contrast to several other species, notably some of the dabbling ducks, Pochard numbers often remained quite constant for relatively long periods, suggesting a low turnover of individuals.

Tufted Duck *Aythya fuligula* (Figure 11). The Tufted Duck's seasonal presence at the lake showed similarities to that of the Common Pochard. Autumn numbers were lower in 2006, and both spring and autumn numbers were lower in 2007 than in 2004 and 2005. Winter numbers were high in 2004/2005 and also in 2005/2006 until the lake froze in the first week of January. During the mild winter of 2006/2007, when the lake remained open, relatively few Tufted Ducks were recorded.

Common Goldeneye *Bucephala clanga* (Figure 12). Goldeneyes were present at the lake yearround but their number in summer never exceeded 15 individuals. Birds in summer were immature. The species starts spring migration early, tracking

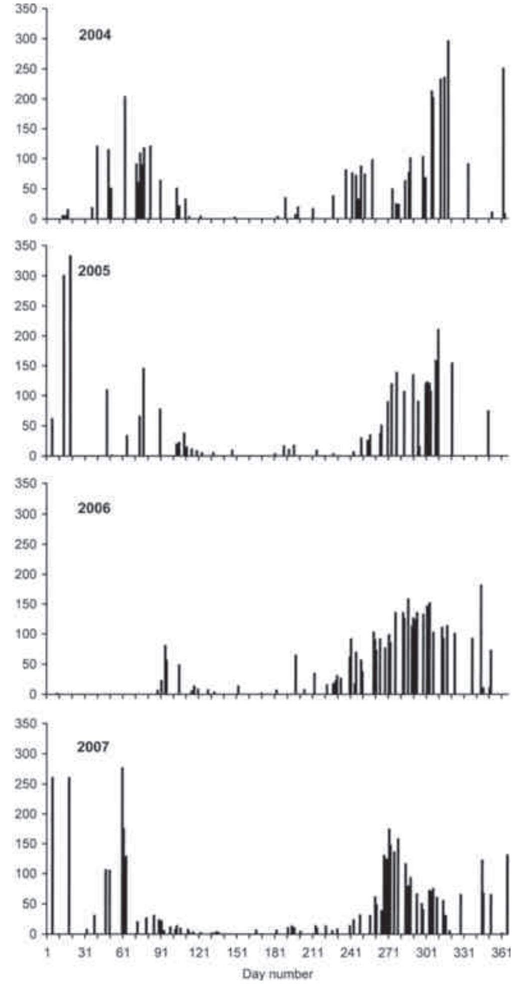

Figure 10. The seasonal occurrence of Common Pochard at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av brunand i Krankesjön åren 2004–2007.

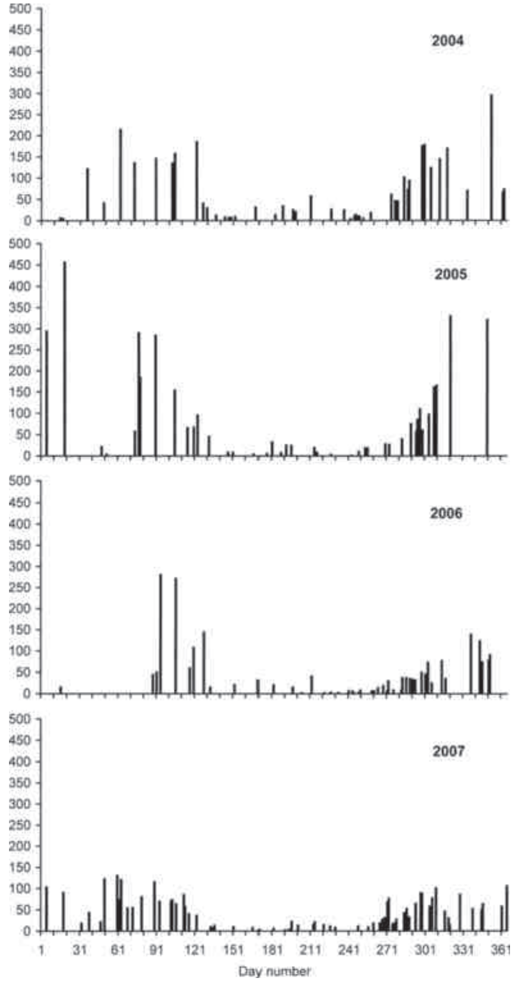

Figure 11. The seasonal occurrence of Tufted Duck at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av vigg i Krankesjön åren 2004–2007.

ice break-up as this advances northward, and peak numbers occurred in February–March. Numbers in autumn started a gradual build-up at the beginning of October and reached more than 300 by mid-December in 2004 and 2005. Numbers remained high over the winter 2004/2005 until the lake froze in the last week of January (a pattern shared with Mute Swan, Pochard and Tufted Duck).

Smew *Mergus albellus* (Figure 13). Smew occurrence showed a pattern similar to that of Goldeneye, with the highest number in February to the first week of April, but numbers never exceeded 100 individuals during the four years. Autumn numbers started to increase somewhat later in Smew than in Goldeneye.

Goosander *Mergus merganser* (Figure 14). Goosander showed a picture almost identical to that of Smew, with a peak from February to the first week of April and an autumn build-up of numbers from about mid-October. Numbers often fluctuated widely between counts (and often also during counts) as flocks entered or left the lake.

Common Coot *Fulica atra* (Figure 15). The general pattern of Coot numbers was relatively similar during three of the four years, with a spring peak by mid-March and low numbers during May and June (breeding season). The date when juveniles were included in the totals varied somewhat between the four years but had no appreciable effect on the curve of gradual build-up of numbers; this normally took place from July to late October. The year 2006 deviates from this pattern. The normal spring peak may have failed to appear because of the late ice break-up, but also numbers in autumn were much lower than in the other three years (see below).

Between-year population fluctuations

In this section we present the inter-annual variations in the numbers of the different waterbird species recorded during the whole study period from summer 1985 to December 2007, with the main focus on the autumn, for which most data are available.

Great Crested Grebe (Figure 16). During the first census years, the number of adult Great Crested Grebes was extremely low but then showed a steady increase to a peak during the first half of the 1990s. This period was followed by slightly lower numbers during the following years. However, the latter period contains the two gaps in the census series, so the exact form of the population curve is unknown. Since then, peak numbers in summer have been relatively high, with some variation between years. Non-breeding adults have most likely occurred in some of the earlier years, but this cannot be established with certainty from available maps and notes. During the last few years, however, up to 90, probably partly non-breeding, adult grebes have formed fishing-flocks roaming widely over the lake in summer (Källander 2008).

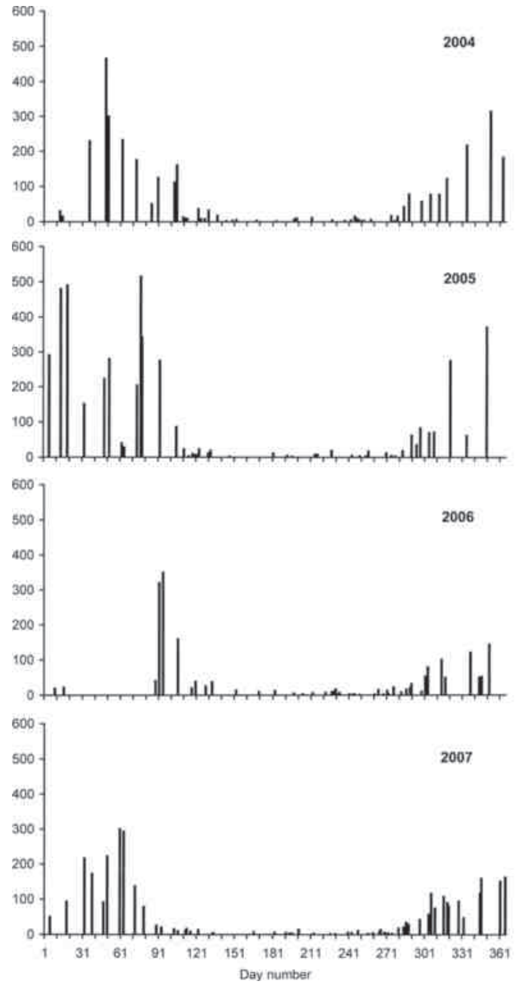

Figure 12. The seasonal occurrence of Common Goldeneye at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av knipa i Krankesjön åren 2004–2007.

Great Cormorant (Figure 17). As in Sweden as a whole and in much of continental Europe (Bregnballe et al. 2003), the number of Great Cormorants observed at Lake Krankesjön increased during the study period ($r_s = 0.893$, $N = 21$, $P<0.001$). During the first five years, less than 10 cormorants were recorded during September–October each year and almost none in spring. By 2007, some 40–50 Cormorants were present daily at the lake during autumn, and smaller numbers were also present throughout spring and summer. During the last few years Cormorants also took to roosting at night in willow trees at the mouth of the small stream that enters the lake from the southeast. As mentioned above, this roost was, at least sometimes, also used by birds that arrived from other areas. The highest total observed at the roost (102 individuals), as well as exceptional numbers caused by temporarily staging flocks (see above) have not been included in Figure 17 or the analysis of the population trend.

Whooper Swan. During the first ten or so years of the study, single pairs of Whooper Swan bred in the vicinity of the lake, and 2–4 birds were sometimes seen on the lake during summer. This has since changed. Thus, during 1985–1999 Whooper

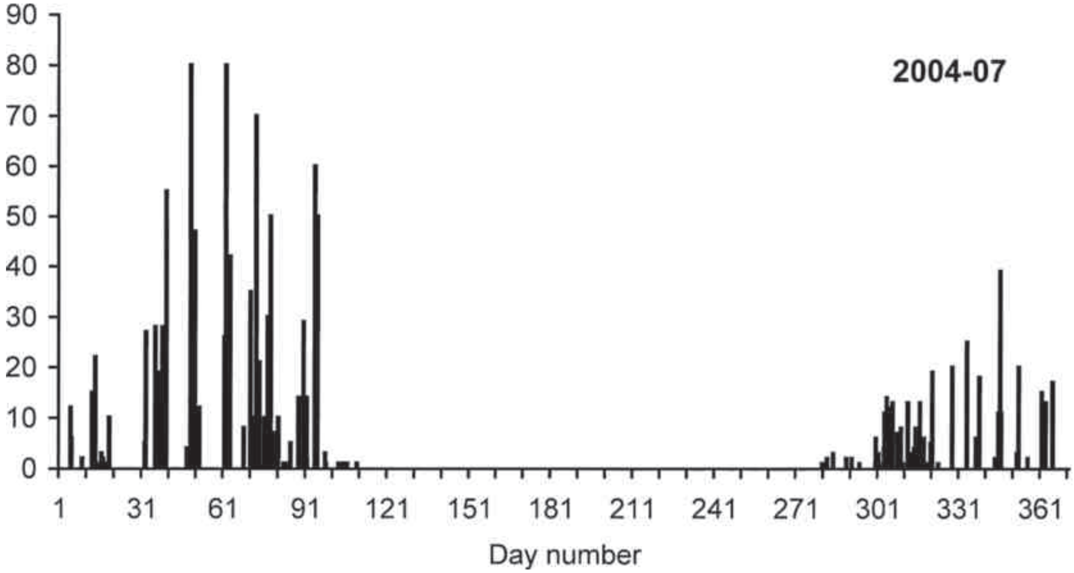

Figure 13. The seasonal occurrence of Smew at Lake Krankesjön. Combined data for 2004 to 2007.
Den årstidsmässiga förekomsten av salskrake i Krankesjön. Kombinerade data för åren 2004–2007.

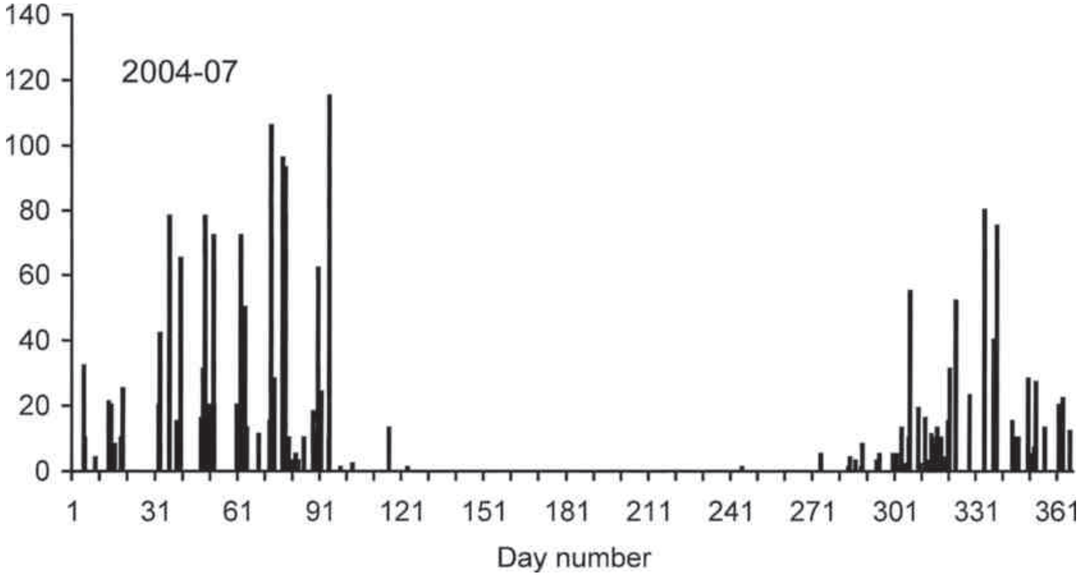

Figure 14. The seasonal occurrence of Goosander at Lake Krankesjön. Combined data for 2004 to 2007.
Den årstidsmässiga förekomsten av storskrake i Krankesjön. Kombinerade data för åren 2004–2007.

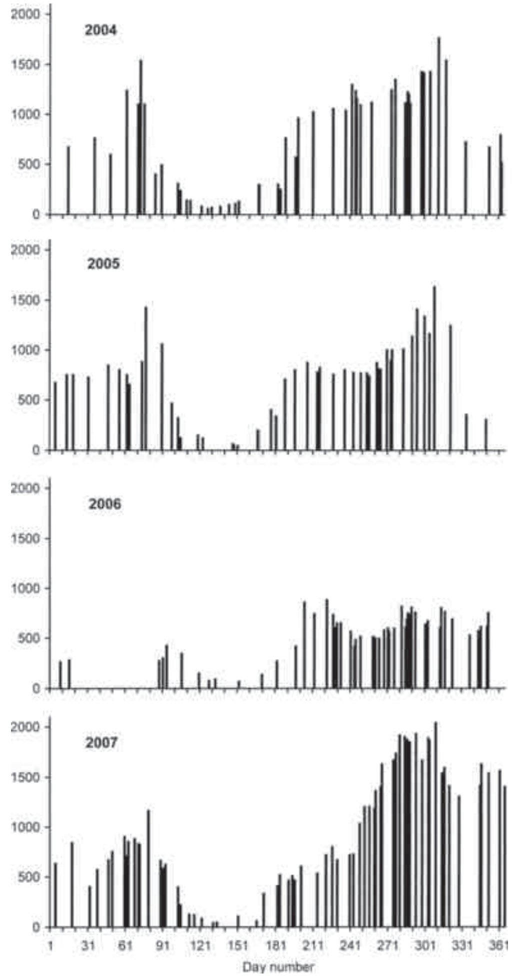

Figure 15. The seasonal occurrence of Common Coot at Lake Krankesjön in 2004 to 2007.
Den årstidsmässiga förekomsten av sothöna i Krankesjön åren 2004–2007.

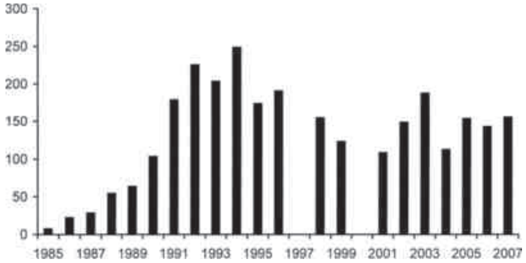

Figure 16. The highest number of Great Crested Grebe recorded in July at Lake Krankesjön in each of the study years 1985–2007. Note the very low numbers during the first years.
Högsta registrerade antal skäggdoppingar i Krankesjön i juli under vart och ett av åren 1985–2007. Notera de mycket låga antalen i periodens början.

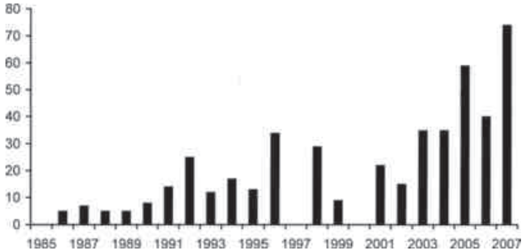

Figure 17. The highest number of Great Cormorants recorded during September–October at Lake Krankesjön in each year 1985–2007. Brief visits by migrating flocks are not included.
Högsta antalet skarvar i Krankesjön under september–oktober under vart och ett av åren 1985–2007. Tillfälliga besök av flyttande skarvar har uteslutits.

Swans were observed on the lake on 18 out of 75 census days (24%) during June–August. During the same months in 2003–2007, Whooper Swans were only seen on 3 out of 59 days (5%). In October during the first two years, from 20 to almost 50 Whooper Swans were feeding at the lake, and at least in 1986 some of them probably were staging there for weeks. Although Whooper Swans have been seen on the lake in October and November during the last four years, their visits have been short. In fact, on a couple of occasions flocks have arrived from the east, landed on the lake only to leave within an hour or two. In autumn 1986, Whooper Swans fed on the tubers of *Potamogeton pectinatus*, which was the first of the submerged plants to recolonize and which in 1986 covered about half of the lake's bottom in sparse stands (Andersson et al. 1990, Hargeby et al. 1994). Subsequently, this plant was largely replaced with charophytes. *Potamogeton pectinatus* tubers are an important food of both Whooper and Bewick's swans *Cygnus columbianus* (Schneider-Jacoby et al. 1991, Beekman

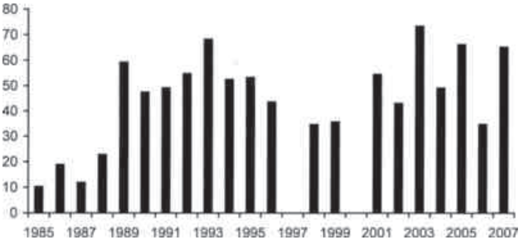

Figure 18. The mean number of Mute Swans at Lake Krankesjön during May to October in 1985–2007. To account for differences in census frequency, the figures are means of the mean for each of the six months.
Medelantal knölsvanar på Krankesjön för månaderna maj–oktober åren 1985–2007. För att ta hänsyn till skillnader i besöksfrekvens är värdena medeltal av månadsmedelvärdena.

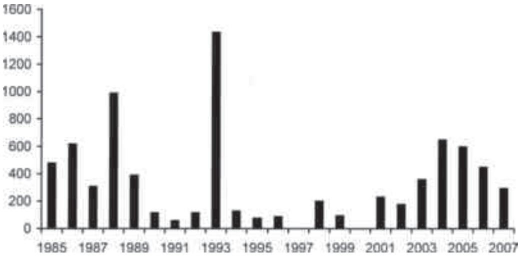

Figure 19. The highest number of European Wigeon recorded during September–October at Lake Krankesjön in each year 1985–2007.
Högsta registrerade antal bläsänder i Krankesjön under september–oktober under vart och ett av åren 1985–2007.

et al. 1991), so the near disappearance of this food resource can no doubt explain the lower numbers of Whooper Swan on the lake in recent years.

Mute Swan (Figure 18). The number of breeding pairs of Mute Swan during the period seems never to have exceeded eleven, so the majority of swans recorded on the lake have been non-breeders. The Figure shows adult and almost adult (all-white) swans during May through October. The pattern is rather similar to that for the Great Crested Grebe, i.e. very low numbers in the early years rising to a peak around 1993, then falling off only to increase again after 2000, however with low numbers in 2006 (see below). The peak in 2003 was caused by exceptionally high numbers of swans being present during the whole of May, with a maximum of 230 on the 24th.

European Wigeon (Figure 19). The maximum number of Wigeon varied much in September and October from 1985 to 2007. There was a peak in 1993 followed by several years with low numbers until 2001. The pattern is very similar if mean counts are used.

Mallard. Mallard numbers were highest in winter, November–February, a period from which counts are quite few before 2004. The highest number, 1700, was recorded in mid-January 1993, but 700 birds or more were seen in an additional eleven winters. However, the data do not allow any conclusion about either fluctuations or trends in number. Mallards do not seem to feed much at the lake, at least not during the day, but use reed edges

Mute Swan Knölsvan

Pochard Brunand

and, when the lake is ice-covered, the ice next to open parts as loafing sites. Probably they feed in agricultural fields at night.

Gadwall (Figure 20). A few Gadwalls were seen in the period April to June in all but three years, but the highest numbers were recorded in September and October (cf. Figure 7). Although there was much variation among years, Gadwall numbers show a positive trend over the study period ($r_s = 0.658$, $N = 21$, $P<0.02$).

Northern Pintail. Although Pintails were recorded in all years, numbers were low, particularly in spring (highest spring number 21; normally just a few). Numbers in autumn were somewhat higher, with top records of 121 and 55, but flocks of more than half a dozen birds were highly fortuitous. For this reason nothing can be said about either trends or fluctuations in number.

Northern Shoveler (Figure 21). The maximum spring number varied from no Shoveler observed in spring 1998 to 35 (in three years), while the corresponding autumn figures ranged from two (1991) to 140 (2005). Both spring and autumn numbers thus show considerable variation. Relatively high numbers were present in autumn during 1987–1990, but generally there is no discernable pattern in Shoveler occurrence at the lake during the study period.

Common Teal (Figure 22). The highest spring numbers of Teal were always found in April, but since counts in many years did not start until mid-April, the peak occurrence may well have been missed in some phenologically early years. For that reason it is doubtful whether the recorded peak numbers before 2004 (varying from eight in 1998

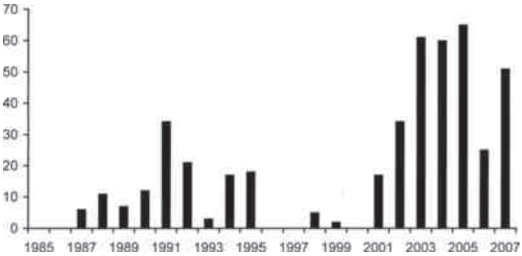

Figure 20. The highest number of Gadwall recorded during August–October at Lake Krankesjön in each year 1985–2007.
Högsta registrerade antal snatteränder i Krankesjön under augusti–oktober under vart och ett av åren 1985–2007.

Coot Sothöna

to 96 in 1988) mirror the species' true presence on the lake. Also autumn numbers show a good deal of variation, with peaks in 1993 and 2006. Means for August through October in these two years were about 100 and 80 birds, and peak numbers 300 and 610.

Garganey. The Garganey is the rarest of the dabbling ducks breeding in Sweden, and its numbers are said to vary strongly between years (Svensson et al. 1999). The highest numbers during the study period were recorded in 1990, when nine individuals were seen on 26 April, six on 1 June, and four on 12 July. In autumn, the species was seen in only six of the years.

Common Pochard (Figure 23). Autumn numbers of Pochard on the lake show a statistically significant negative trend. This holds regardless of whether maximum autumn numbers ($r_s = 0.562$, $N = 21$, $P<0.02$) or weighted means for the autumn months are used ($r_s = 0.652$, $N = 21$, $P<0.02$). How-

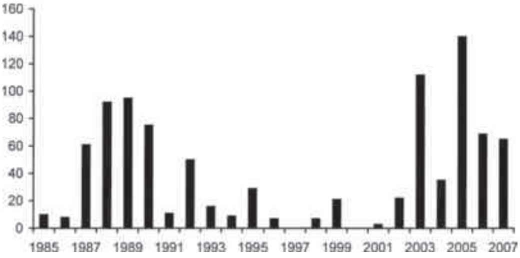

Figure 21. The highest number of Northern Shoveler recorded during August–October at Lake Krankesjön in each year 1985–2007.
Högsta registrerade antal skedänder i Krankesjön under augusti–oktober under vart och ett av åren 1985–2007.

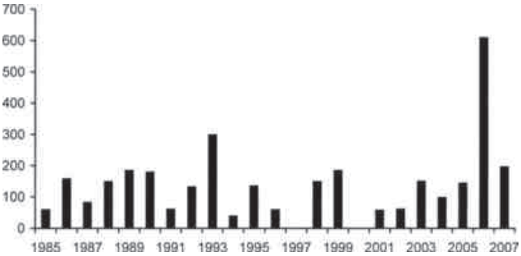

Figure 22. The highest number of Common Teal recorded during August–October at Lake Krankesjön in each year 1985–2007.
Högsta registrerade antal krickor i Krankesjön under augusti–oktober under vart och ett av åren 1985–2007.

ever, as seen in the diagram, the trend was caused by a decrease that took place during the first ten years, after which numbers have remained fairly stable. In most years, counts were started too late in spring to cover the period when numbers peak, which occurs in March (cf. Figure 10).

Tufted Duck. As seen from Figure 11, the highest numbers of Tufted Duck occur during November through March when no counts were carried out in most years, which precludes analysis of population trends and fluctuations. In those earlier years from which data are available, numbers were more than three times higher in February–March than in November–December (highest number 970 on 15 February 1990).

Common Goldeneye. The same problem as for the Tufted Duck applies to the data for Goldeneye, viz. that too few counts were carried out during the winter months. However, the number of Goldeneye seems to have increased during the study period in line with the positive trend shown for wintering birds (Nilsson 2008). Thus, peak numbers in March in 1988–1991 were only a fifth of those in 2004–2007.

Smew. As for the previous two species, the material does not permit any conclusions regarding either trends or fluctuations because of the scarcity of winter data in most years. Numbers in February–March (Figure 13) reached 80 individuals in 2004 and were higher in late winter than in autumn in all but one year for which these two periods could be compared.

Goosander. Goosanders visit the lake almost exclusively during October to early April (Figure 14) and useful data therefore only exist for the last four years. The highest count during the study period was 256 individuals on 14 April 1986; numbers just exceeded 100 twice.

Common Coot (Figure 24). During the whole study period, the Common Coot was the most numerous waterbird on the lake almost year-round, with nearly 2500 individuals in autumn 1993. Numbers were very low in the first years but increased rather quickly to reach a peak in 1993 after which they again fell. From 2001 onwards numbers have been comparable to those in the early 1990s, with the exception of 2006, when the population in autumn was only about half that of the preceding years. The dynamics of the Coot population thus shows strong similarities to that of the Mute Swan (and to some extent to that of the Wigeon and Great Crested Grebe).

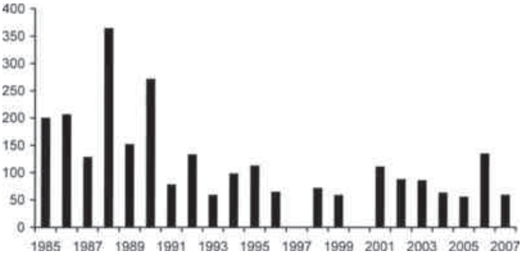

Figure 23. Mean number of Common Pochard recorded during August–October at Lake Krankesjön in each year 1985–2007.
Medelantal brunänder på Krankesjön under perioden augusti-oktoberunder vart och ett av åren 1985–2007.

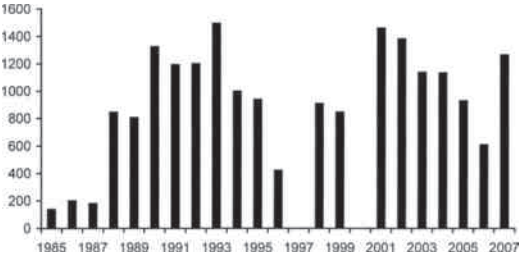

Figure 24. The highest number of Common Coot recorded during August–November at Lake Krankesjön in each year 1985–2007.
Högsta registrerade antal sothöns i Krankesjön under augusti–oktober under vart och ett av åren 1985–2007.

Discussion

Lake Krankesjön as a moult and stop-over site

Figures 1–15 clearly show that the species treated in this paper are most numerous during the migration periods or, for some of the species, during winter. For Coot and Mute Swan, high numbers are also present during moult. From a conservation perspective, the lake is important because of its small breeding colony of Black Terns *Chlidonias niger* beside a few other relatively sparse species (Bittern *Botaurus stellaris*, Penduline Tit *Remiz pendulinus*, etc.). However, few species of waterbird breed at the lake, and those that do so breed in low or moderate numbers. The most common breeding waterbirds, apart from a (re-established) colony of Black-headed Gull *Larus ridibundus*, are Coot, Great Crested Grebe, Mute Swan, Greylag Goose *Anser anser* and Common Tern *Sterna hirundo*. In recent years, a single Tufted Duck brood has been seen in two seasons and in each year one or two Mallard broods, but there are only a few breeding records for other dabbling ducks (Gadwall, Garganey). So, clearly the lake's main importance is as a moulting and staging area. The number of Coot at Lake Krankesjön in summer and autumn, for instance, is among the highest for any lake in Sweden, with the exception of Lakes Tåkern and Hornborgasjön (Nilsson 2007, L. Nilsson, pers. comm.).

To get some reference against which Lake Krankesjön's importance as a stop-over site in autumn could be compared, we searched the Swedish bird database, Svalan (http://artportalen.se/birds/), restricting our search to observations made in South Sweden (Götaland) during the period 1 August to 31 October in 2004–2008. For each species, we specified a minimum number that should be exceeded for an observation to be included (e.g. 1000 for Wigeon, 100 for Gadwall). A number of localities were identified from which high autumn numbers of one or more waterbird species had been reported consistently. These were, however, predominantly sheltered bays along the coast. Among inland sites, Lakes Tåkern and Hornborgasjön stood out from all the others by holding numbers several times higher than any other South Swedish lake (also cf. Nilsson 2007). For single species, higher numbers than those recorded at Lake Krankesjön had been reported from a few lakes. While, on the whole, the exercise failed to establish Lake Krankesjön's exact position among South Swedish lakes based on its importance as a moulting and staging site, it is probably safe to conclude that Lake Krankesjön is one of the more important ones, especially considering the scarcity of shallow, vegetation-rich and productive lakes in Sweden south of Lakes Tåkern and Hornborgasjön.

Causes of fluctuations in the lake's waterbird numbers

An unknown part of the between-year fluctuations in numbers depends on deficiencies in the counts themselves (individual birds or even flocks having gone undetected, or birds being counted twice). Another factor that may have had some influence on the reliability of the data is that counts were carried out only twice a month for most of the period, with a few gaps here and there. Most likely neither of these two sources of error is particularly important, however, at least for those species that show the most regular occurrence on the lake, such as Great Crested Grebe, Mute Swan, Pochard and Coot. We therefore focus here on the dynamics of these species, although some comments are made also on the occurrence of a few others.

Another factor that might cause variation in the number of staging birds at a locality is if the availability of suitable areas in the surroundings varies between years. To some extent this has been the case during the present study. In autumn 2006, for instance, the nearby Vombs ängar Nature Reserve, only about 3 km distant, was flooded and attracted large numbers of dabbling ducks, particularly Teal, Shoveler and Wigeon. An exchange of individuals between this locality and Lake Krankesjön was documented and may at least explain some of the day-to-day variations in numbers on the lake. Ducks have also been seen travelling between Lake Krankesjön and other locations in its neighbourhood.

Fluctuations in water level could potentially be an important factor affecting the number of dabbling ducks staging on the lake, because high water levels could make the submerged vegetation unavailable to species feeding by up-ending. However, probably this would mainly affect Gadwall, Pintail and Shoveler, perhaps also to some extent Wigeon. Mallard were sometimes seen foraging by up-ending in shallow parts of the lake close to their loafing sites during daytime, but their main feeding probably took place in terrestrial habitats at night. Gadwall was the species most regularly seen feeding (by up-ending) during autumn. Also Wigeon were sometimes seen using up-ending as a foraging method, but in autumn and winter Wigeon appeared not to forage much during the light hours. Sometimes, however, they associated with flocks of Coot, but this was much more pronounced in spring. Coots dive and bring plant material to the surface that would otherwise be unavailable to the Wigeon, and Wigeon use material that the Coots drop while feeding. This commensal association was very frequent in spring and sometimes practically all of up to 200 Wigeon were using Coots in this way (HK unpubl. data).

One cause of numerical fluctuations and trends can be searched on a 'global' level, i.e. population changes involving large portions of a species' total population. The trend in number of Great Cormorants that used Lake Krankesjön no doubt is best explained by this species' general increase practically everywhere in Europe, including Sweden (Engström 2001, Bregnballe et al. 2003). Among the other species treated here, the Gadwall showed a statistically significant positive trend over the study period. This reflects a well-documented general increase and an expansion of the species' breeding area in Sweden during the last 60 years. In 1944, the breeding population in Sweden was estimated at 60–70 pairs (SOF 1962) and in 2003 at 675–725 pairs (SOF 2004). In autumn 2005, a total of 2300 Gadwall were counted while staging on three shallow lakes in South and South Central Sweden (SOF 2006). In contrast, autumn numbers of Pochard at Lake Krankesjön showed a negative trend during the first ten years but have since remained relatively constant. Unfortunately, Swedish September data from the international waterbird counts (Nilsson 2007) do not permit a calculation of an index with which the data from Lake Krankesjön could be compared.

The fluctuation patterns of Great Crested Grebe, Mute Swan and Coot were mutually rather similar, despite the fact that the grebe is piscivorous and the other two feed almost entirely on submerged plants (Cramp 1977, 1980). In fact, there were statistically significant correlations between numbers of grebes and swans ($r = 0.703$, df 19, $P<0.001$), swans and coots ($r = 0.795$, df 19, $P<0.001$) and also numbers of grebes and coots varied in parallel ($r = 0.461$, df 19, $P<0.01$).

The winter survival of Coots has been shown to be affected negatively by the severity of the winter, expressed as number of days with ice (Cavé & Visser 1985). The number of Coots at Lake Krankesjön during 1985–2007 correlated positively with January temperatures measured at Malmö ($r = 0.710$, $P<0.001$), as did the number of Mute Swans ($r = 0.602$, $P<0.01$), whereas the correlation for Great Crested Grebe was low ($r = 0.228$) and non-significant. The question is whether winter temperatures influence the numbers of these waterbird species directly or via effects on their food supply.

By using an ordination method, Milberg et al. (2002) analysed the relationship between biomass of submerged plants and numbers of birds staging on Lake Tåkern, southern Sweden, in mid-September. They found a negative relationship between plant biomass and numbers of the piscivorous Cormorant and Goosander, but not with the likewise piscivorous Great Crested Grebe, which showed a clear positive relationship with plant biomass. For some predominantly herbivorous species (Coot, Pochard, Mute Swan, Mallard and Wigeon in particular) there was a very strong positive association between numbers and the amount of submerged plants.

Unfortunately, measurements of the extent of submerged vegetation at Lake Krankesjön exist for only 11 of the 21 years that its waterbird populations were monitored. For the three species, Great Crested Grebe, Mute Swan and Coot, the correlations between submerged vegetation and population size are nonetheless statistically significant (Great Crested Grebe, $r = 0.897$, $P<0.001$; Mute Swan, $r = 0.794$, $P<0.05$; Coot, $r = 0.949$, $P<0.001$) demonstrating that the same relationship as found at Lake Tåkern existed also at Lake Krankesjön. The relationships between biomass of submerged plants and other (inter-correlated) limnological variables, such as transparency (Secchi depth) and chlorophyll (a measure of the amount of micro-algae), which likely influence the growth of submerged vegetation, will be treated elsewhere. However, it is worth noticing that the population fluctuations of all three of the above-mentioned waterbird species show statistically significant correlations with measures of transparency and algal mass (for which respectively 20 and 19 years of data exist). In agreement with Milberg et al. (2002) we therefore conclude that waterbird numbers at Lake Krankesjön were strongly influenced by water quality via its effects on the submerged vegetation.

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Sammanfattning

Krankesjön c.20 km öster om Lund blev känd genom boken Krankesjön – ett fåglarnas paradis (Swanberg 1931) och inte minst genom den koloni av svarthalsade doppingar *Podiceps nigricollis* som Swanberg fann där. Kolonin tycks ha försvunnit under andra hälften av 1930-talet, men sjön fortfor att vara en god fågelsjö. Under åren 1974–1976 inträffade emellertid en dramatisk minskning i flera fågelarters numerär, t.ex. skäggdopping *Podiceps cristatus*, knölsvan *Cygnus olor* och sothöna *Fulica atra*. Parallellt härmed skedde stora förändringar i sjöns vegetation och vattenkvalitet. Från att ha varit förhållandevis klart blev vattnet grumligt samtidigt som bottenvegetationen försvann nästan helt (Karlsson m.fl. 1976). Detta tillstånd tycks ha varat ungefär till 1985, då en återgång till tidigare förhållanden inleddes (Andersson m.fl. 1990). Samma år, 1985, startade framlidne Gunnar Andersson regelbundna räkningar av Krankesjöns simfåglar. Räkningarna, vilka fortfarande pågår, syftade till att finna samband mellan fågelförekomsterna och olika limnologiska variabler. Resultaten av dessa räkningar presenteras i denna uppsats.

Metod och studieområde

Krankesjön är c. 3,4 km^2 och mycket grund. Medeldjupet är ungefär 1,5 m, det djupaste partiet når 3 m, men stora områden har ett djup betydligt mindre än 1 m. Undervattensvegetationen domineras helt av kransalger *Chara* sp.; några mindre områden hyser borstnate *Potamogeton pectinatus*. Sjön kantas av en bård av vass *Phragmites australis*, som i väster bildar bredare fält och i sjöns sydöstra hörn större sammanhängande områden. Sjön saknar öar, men har i sin östra del ett antal isolerade vassruggar och partier av annan vegetation (kalmus *Acorus calamus*, igelknopp *Sparganium* sp., m.m.). Två fågeltorn finns vid sjön, ett på den södra sidan (det s.k. Almentornet) och ett i öster (Silvåkratornet). Sjön har två små tillflöden, Silvåkrabäcken i sydost och Länsmansbäcken i sydväst och avvattnas till Kävlingeån via Ålabäcken på sjöns nordsida.

Räkningarna av sjöns simfåglar utfördes från de båda fågeltornen med hjälp av tubkikare. Under åren 1985–2003 genomfördes i allmänhet två räkningar per månad, begränsade till perioden mitten av april–mitten av oktober, men vissa år utfördes räkningar också övriga månader. Två luckor finns i detta material, nämligen för åren 1997 och 2000. Från och med 2004 har räkningar genomförts under hela året och betydligt oftare än tidigare (Tabell 1). Under dessa fyra år räknades dock inte alltid samtliga arter vid varje besök (dock oftast flertalet). Parallellt med räkningarna av simfågel har olika limnologiska undersökningar genomförts i sjön.

Givetvis är de siffror som erhållits under simfågelräkningarna behäftade med viss osäkerhet. Vissa arter, t.ex. skäggdopping, underskattas lätt under blåsiga förhållanden, gräsänder *Anas platyrhynchos* ligger under dagtid ofta inne i vass och annan vegetation och blir ofta synliga först då de skräms ut på öppet vatten av exempelvis havsörn *Haliaaetus albicilla*. Speciellt under flyttningstider sker också en viss omsättning av fågel i sjön, vilket kan leda till ganska stora variationer från en dag till en annan. Vi är dock övertygade om att de resultat som redovisas här ger en rättvisande bild av såväl de säsongsmässiga som de årliga fluktuationerna i sjöns simfågelfauna. Inte minst torde detta gälla de arter, som är närvarande i sjön under långa perioder och i ganska konstanta antal, främst skäggdopping, knölsvan och sothöna.

Redovisningen omfattar inte samtliga arter som räknats; exempelvis ingår inte hägrar, gäss och måsfåglar och inte heller de olika mer eller mindre sällsynta arter som uppträtt under perioden.

De vunna resultaten redovisas under två rubriker, årscykeln respektive beståndsvariationerna. Den förra avser att spegla de olika arternas säsongsmässiga förekomst vid Krankesjön, vilket i huvudsak sker i form av en serie diagram med tillhörande kommentarer. Denna del är uteslutande baserad på de senaste fyra årens räkningar, vilka utförts tillräckligt frekvent för att en bild skall framträda. Under den andra rubriken visas beståndsutvecklingen för de olika simfågelarterna under hela perioden 1985–2007.

Årscykeln

För flertalet arter visas det säsongsmässiga uppträdandet i sjön i figurer, med separata diagram för vart och ett av de fyra åren. Härvid har eftersträvats att ha samma skala på de olika delfigurerna, men för en art, krickan *Anas crecca*, har detta inte följts. Vidare har de fyra åren slagits samman för sex arter. På tidsaxeln (x) anges dagnummer, dvs den 1 januari = 1, 31 december = 365 (ingen hänsyn till skottår) och 1 juli således = 182. Y-axeln saknar av tekniska skäl etikett, men anger antalet individer. För ytterligare några få arter ges bara en kort presentation i texten.

Skäggdopping *Podiceps cristatus* (Figur 1). Den milda vintern 2006/2007 övervintrade några få skäggdoppingar, men normalt anlände de första skäggdoppingarna i samband med islossningen eller, isfria år, vid ungefär samma tid (första halvan av mars) för att därefter snabbt öka i antal. Antalet var högt över sommaren, c. 130–150 ex., varav en troligen ganska hög andel utgjordes av icke-häckande, och minskade sedan successivt från mitten av september. Efter mitten av november var ytterst få doppingar kvar i sjön – i stark kontrast till förhållandena på den närbelägna Vombsjön, där antalet ökar i november för att årligen uppgå till c. 2000.

Storskarv *Phalacrocorax carbo* (Figur 2). Antalet skarvar var normalt lägre under våren–sommaren än under hösten. De tre högsta siffrorna avser flyttande flockar, vilka högst tillfälligt landat på sjön och fiskat innan de dragit vidare. Den höga siffran (102) den 2 november (2007) är fåglar som uppsökt sovplatsen i pilträd vid Silvåkrabäckens mynning och inkluderar även fåglar, som anlände från andra håll än själva sjön.

Sångsvan *Cygnus cygnus*. Arten ses inte särskilt ofta i sjön, men rastar tillfälligt framför allt i mars och slutet av oktober–början av november, då upp till 30 fåglar setts. Också vintertid ses en del sångsvanar, men arten söker då sin föda huvudsakligen i åkermarken, på raps eller ung stråsäd.

Knölsvan *Cygnus olor* (Figur 3). Figuren visar endast antalet utfärgade knölsvanar (vilka alltid kraftigt dominerar antalsmässigt). Antalet häckande par tycks aldrig ha överstigit 11 (och var under de fyra åren ännu lägre), varför det i huvudsak handlar om icke-häckande fåglar. Som synes är mönstret de olika åren ganska olikartat. Den totala avsaknaden av knölsvanar från januari till slutet av mars 2006 beror på en sen, men total isläggning av sjön, men noterbart är de låga antalen även under resten av året (se nedan). År 2007 ökade antalet knölsvanar mycket starkt under senhösten, en ökning som fortsatte in i januari 2008 (220 ex den 21).

Bläsand *Anas penelope* (Figur 4). Bläsanden visar ganska tydliga toppar under artens sträcktider, men dessutom registrerades mycket höga antal i december och januari under ett par av åren. Således skedde under november–december 2006 och 2007, dvs efter artens normala sträcktid, en stark inflyttning av bläsänder till sjön, vilken i januari 2007 resulterade i att över 900 ex. noterades. Isläggning i senare delen av januari detta år tvingade bläsänderna att tillfälligt lämna sjön. Notera också den nästan totala avsaknaden av bläsänder våren 2006 också efter det att isen gått upp i slutet av mars.

Gräsand *Anas platyrhynchos* (Figur 5). Figuren sammanfattar förekomsten under de fyra åren. Normalt sågs de högsta antalen gräsänder under senhöst och vinter, medan ytterst få gräsänder sågs under häckningstid. Antalen ökade sedan sakta under sommaren med en del ruggande fåglar och därefter ganska gradvis under hösten.

Stjärtand *Anas acuta* (Figur 6). Stjärtanden är normalt så sporadisk och fåtalig i Krankesjön, speciellt om våren, att de fyra årens data lagts samman i figuren. Hösttoppen sammanfaller väl med artens sträckperiod.

Snatterand *Anas strepera* (Figur 7). De milda vintrarna 2006/2007 och 2007/2008 sågs enstaka snatteränder. Under våren var antalen ganska blygsamma, varefter antalen ökade under sommaren och oftast nådde en topp en vecka in i september. Liksom för knölsvan och bläsand var antalet snatteränder något lägre 2006 än de andra tre åren.

Skedand *Anas clypeata* (Figur 8). Liksom för övriga simänder var antalen om våren avsevärt lägre än under hösten. De högsta vårsiffrorna noterades under den andra halvan av april. Mönstret för höstförekomsten skiljer sig ganska markant åt mellan åren med en tidigare topp 2006 och 2007 än de båda föregående åren.

Kricka *Anas crecca* (Figur 9). Lägg märke till att skalorna i de två nedre delfigurerna skiljer sig markant från skalan i de båda övre. Den helt uteblivna vårtoppen 2006 kan möjligen tillskrivas det faktum att sjön inte blev helt isfri förrän en bit in i den första aprilveckan. Liksom för bläsand skedde i december 2006 en stark inflyttning av kricka till sjön och antalet kulminerade i januari 2007 med c. 2000 ex., vilka låg tillsammans med bläsänderna ute på öppet vatten.

Årta *Anas querquedula*. Årtan är sjöns sällsyntaste simand och sågs normalt blott med några få exemplar i april och maj, med en liten topp kring 1 maj. De mycket få höstobservationerna gjordes i augusti och september.

Brunand *Aythya ferina* (Figur 10). Bortsett från övervintrande fåglar vissa år, var mönstret för brunandens uppträdande ganska likartat mellan åren. De låga vårsiffrorna 2006 kan troligen hänföras till den sena islossningen. Högstaantalen var något högre hösten 2004 än de andra tre åren, då de låg kring 150 ex. Brunänderna låg oftast inom ett begränsat område utanför den norra stranden.

Vigg *Aythya fuligula* (Figur 11). Viggens uppträdande uppvisade ganska stora likheter med brunandens, inklusive januariförekomsten 2005, men uppgången i antal om hösten inträffade senare än för brunanden. De registrerade antalen under 2007 ligger av okänd anledning något lägre än de andra årens.

Knipa *Bucephala clanga* (Figur 12). Sommartid var antalet knipor i Krankesjön mycket lågt och utgjordes av yngre, icke-häckande fåglar. Antalen ökade normalt ungefär från början av oktober. I vilken utsträckning knipor övervintrade bestämdes av issituationen; antalen uppgick, som framgår av figuren, under januari och februari under två av åren till c. 500. Vårsträcket var i allmänhet avslutat kring mitten av april.

Salskrake *Mergus albellus* (Figur 13). Salskrakens uppträdande i sjön liknar knipans om man bortser från att arten saknades helt under sommarhalvåret. Antalen var högre under årets tre första månader än under de två sista, med en viss topp i slutet av mars med upp till 80 ex.

Storskrake *Mergus merganser* (Figur 14). Bilden för storskraken är nästan identisk med den för salskraken, dvs med förekomst från början av oktober till början av april. Antalen växlade ofta ganska starkt mellan räknetillfällena och grupper sågs både lämna sjön och anlända till den.

Sothöna *Fulica atra* (Figur 15). Det allmänna mönstret var ganska likartat åtminstone för tre av åren: ganska betydande antal övervintrande fåglar, ökande antal till mitten av mars och därpå en minskning ungefär till mitten av juni. Därefter ökade antalen för att nå en topp i början av november. 2006 avviker så till vida att sothöns saknades från mitten av januari till slutet av mars, då sjön var helt istäckt, och genom att hösttoppen i stort sett uteblev.

Beståndsfluktuationer

Här redovisas artvis de förändringar i simfågelbeståndet som registrerats under perioden 1985–2007. Tonvikten ligger på hösten, från vilken flest data föreligger och antalet fåglar varit högst.

Skäggdopping (Figur 16). Under studiens första år var antalet skäggdoppingar extremt lågt men ökade stadigt för att nå en topp under de första åren på 90-talet. Därpå följde en viss nedgång, men beklagligtvis saknas data för åren 1997 och 2000. De senaste 6–7 åren har beståndet varierat något kring en relativt hög nivå. Figuren visar högsta antal adulta fåglar i juli månad och inkluderar åtminstone de senaste åren uppenbarligen ett betydande antal icke-häckare.

Storskarv (Figur 17). I Krankesjön (liksom i Sverige i övrigt och stora delar av kontinenten) visar storskarven en statistiskt signifikant ökning under perioden ($r_s = 0,605$, $N = 21$, $P<0.02$). Under de första åren sågs skarvar praktiskt taget aldrig under våren och höstsiffrorna nådde inte 10 ex. Numera uppehåller sig regelbundet 15–20 skarvar i sjön under vår och sommar och 40–50 under hösten.

Sångsvan. Under de första cirka 10 åren häckade sångsvan i sjöns omgivningar och 2–4 fåglar sågs ibland sommartid på sjön. Här har emellertid en förändring skett. Medan sångsvan under perioden 1985–1999 sågs under 18 av 75 räkningsdagar under juni–augusti (24%), sågs arten endast 3 av 59 dagar (5%) under motsvarande tid åren 2003–2007. Under de första två åren sågs i oktober från 20 till 50 sångsvanar, vilka födosökte i sjön och vilka tycks ha stannat under en längre period. Dessa svanar livnärde sig på borstnatens rotknölar. Borstnaten var den första arten att återkolonisera de kala bottnarna och täckte 1986 ungefär hälften av sjöns bottnar, men ersattes senare av kransalger. Eftersom borstnatens rotknölar är en viktig föda för sångsvan (och mindre sångsvan *Cygnus columbianus bewickii*) är det troligt att den minskade förekomsten av rastande sångsvanar hänger samman med att borstnaten senare ersatts av kransalger.

Knölsvan (Figur 18). Medelantalet adulta (vita) svanar under månaderna maj–oktober (medeltalet vägt för att korrigera för olika räkningsintensitet olika månader) var mycket lågt under de första åren men steg sedan till en topp i början av 1990-talet för att sedan minska en aning igen. Under de senaste sju åren har antalet växlat en del, med lågt antal speciellt 2006, men i övrigt höga totalantal. Toppen 2003 orsakas av mycket höga antal (upp till 230 fåglar) i maj detta år.

Bläsand (Figur 19). Arten visar ett mycket oregelbundet uppträdande under åren. En kraftig topp 1993 följdes av låga siffror ända till 2003.

Gräsand. Som nämnts ovan var gräsandsiffrorna högst under senhöst och vinter, en period varifrån det är sparsamt med räkningar före 2004. Det högsta registrerade antalet utgörs av 1700 i mitten av januari 1993, men under ytterligare 11 vintrar noterades 700 eller fler gräsänder.

Snatterand (Figur 20). Några få snatteränder sågs alla år utom tre under perioden april–juni, men de högsta antalen noterades alltid i september eller oktober. Trots ganska stor variation mellan åren kan en klar ökning noteras (r_s = 0,658, N = 21, P<0,02).

Stjärtand. Som mest noterades 21 (vår) och 121 exemplar (höst), men förekomsten var mycket oregelbunden och inget mönster kan utläsas ur data.

Skedand (Figur 21). Högsta antal på våren varierade från noll 1998 till 35 (tre olika år) medan höstsiffrorna varierade mellan 2 (1991) och 140 (2005), utan synbart mönster.

Kricka (Figur 22). Möjligen startade räkningarna under flera år för sent på våren för att få med toppen i krickans rastning, varför det är osäkert om vårsiffrorna speglar förekomsten (från max 8 ex. 1998 till 96 ex.1988). Höstsiffrorna varierar likaledes kraftigt, med toppar 1993 och 2006. Medelvärdena för augusti–oktober dessa år var mycket lägre, 100 respektive 80, vilket också visar den stora variationen i siffrorna för denna art.

Årta. Det högsta antal som noterades var 9 ex. den 26 april 1990. På hösten sågs arten endast under sex av de 21 åren.

Brunand (Figur 23). Arten visar en statistiskt signifikant minskning under perioden (r_s = 0,652, N = 21, P<0,02), men denna beror helt och hållet på höga siffror under ett antal år i början. Senare har höstsiffrorna varierat ungefär mellan 100 och 200.

Vigg (Figur 11). Antalet viggar är högst under november t.o.m. mars, en period med få räkningar. De räkningar som finns visar mer än tre gånger så många viggar i februari–mars som i november–december (högsta antal 970 den 15 februari 1990).

Knipa. Liksom för viggen föreligger få räkningar under vintermånaderna. Möjligen har antalet knipor i sjön emellertid ökat. För perioden februari–första veckan i april var de högsta noterade antalen fyra gånger högre 2004–2007 än 1986–2003 (data från 10 av åren).

Salskrake. Också för salskraken saknas tillräckligt med vintersiffror för att säga något om eventuella förändringar i antalet fåglar som besökt sjön.

Storskrake. Samma sak gäller storskraken som för föregående art. Det högsta antal som noterades under perioden var 256 ex. den 14 april 1986; två gånger har antalet överskridit 100.

Sothöna (Figur 24). Under hela perioden var sothönan året runt sjöns vanligaste simfågel (med undantag av den högst tillfälliga toppnoteringen för kricka i januari 2007) med nästan 2500 ex. hösten 1993. Antalet sothöns var emellertid mycket lågt under de första åren men ökade stadigt till 1993, varefter det på nytt minskade, dock utan att nå de första årens bottennivåer. Därefter har antalet sothöns på nytt ökat till mellan 1500 och 2000 höstetid. Ett markant undantag utgör hösten 2006, då antalet endast var ungefär hälften av närliggande höstars.

Krankesjön som ruggnings- och rastningslokal

Från ett fågelskyddsperspektiv är Krankesjön som häckningslokal viktig framför allt på grund av dess koloni av svarttärna *Chlidonias niger*, men sjön hyser också en ett antal mindre talrika arter som rördrom *Botaurus stellaris*, pungmes *Remiz pendulinus*, m.fl. Däremot är antalet häckande andfåglar mycket lågt och utgörs, förutom av grågås *Anser anser*, av knölsvan (max 11 par), gräsand (en eller ett par kullar brukar ses) och vigg (en kull noterad vid vardera två tillfällen under den senaste 5-årsperioden). Till dessa kan läggas några andra vattenfåglar: skäggdopping, sothöna, skrattmås *Larus ridibundus* och fisktärna *Sterna hirundo*, samtliga i låga till måttliga antal. Någon enstaka häckning har konstaterats för snatterand och årta. Sjön har således sitt värde huvudsakligen som ruggnings- och rastningslokal. Undantaget Tåkern och Hornborgasjön, är exempelvis antalet sothöns bland de högsta som noterats för insjöar i Götaland och samma sak gäller för knölsvan. Båda arterna drar givetvis nytta av att sjön är grund och rik på undervattensvegetation. Även om Krankesjön inte på långa vägar kan tävla med Tåkern och Hornborgasjön måste den ändå betraktas som en viktig översomrings- och rastlokal för simfåglar, i synnerhet om man beaktar avsaknaden av liknande sjöar i stora delar av Sydsverige.

Orsaker till variationerna i antalet rastande simfåglar

Vilka är då orsakerna till de variationer i simfågelantalen som redovisas i Figurerna 16–24? En sådan kan vara att andra lokaler i sjöns närhet, som Vombs ängar, vissa år varit mera attraktiva som rastlokal än Krankesjön. Detta gäller dock bara under senare år och bara för några av simandsarterna. En annan faktor kan vara sjöns vattendjup, vilket varierat mellan höstarna. Effekterna härav har inte undersökts, men flera av de simandsarter som höstetid rastar i sjön födosöker inte där, åtminstone inte under dagtid. Beståndsförändringar över större områden är ytterligare en faktor som kan ha gett upphov till variationen. Det ökande antalet storskarvar i sjön, t.ex., är uppenbart endast en spegling av artens allmänna ökning i Sverige och större delen av Europa. Samma sak torde gälla för snatteranden, som också ökat markant i Sverige under den aktuella perioden.

De viktigaste orsakerna till ökningen av antalet skäggdoppingar, knölsvanar och sothöns under perioden (Figurerna 16, 18 och 24) torde dock vara att söka i sjön själv. Som nämndes inledningsvis kännetecknades Krankesjön från mitten av 1970-talet till mitten av 1980-talet av grumligt vatten och kala bottnar. Därefter skedde en snabb förbättring av förhållandena, bottnarna återkoloniserades, till en början av borstnate, senare av kransalger, och siktdjupet ökade. Parallellt härmed ökade de nämnda tre arterna för att alla nå en topp de första åren på 1990-talet. Intressant nog råder statistiskt signifikanta korrelationer mellan antalet skäggdoppingar och antalet knölsvanar, mellan antalet knölsvanar och sothöns, samt mellan antalet skäggdoppingar och sothöns, trots att skäggdoppingen är fiskätare, medan knölsvan och sothöna nästan uteslutande livnär sig av vegetabilier.

Milberg m.fl. (2002) analyserade sambandet mellan mängden undervattensvegetation och antalet rastande simfåglar höstetid i Tåkern och fann ett positivt samband mellan mängden vegetation och både växtätare som knölsvan, sothöna, m.fl. och den fiskätande skäggdoppingen. Tyvärr finns mätningar av Krankesjöns bottenvegetation endast för 11 av de 21 åren. Lika fullt är sambandet mellan bottenvegetation och fågelantal statistiskt signifikant för skäggdopping, knölsvan och sothöna. De tre korrelationerna är alla positiva. För siktdjup och mängden mikroalger (mätt som mängden klorofyll i vattnet), faktorer som kan förväntas ha en stark påverkan på bottenvegetationen, existerar data för 20 respektive 19 av åren. Mellan dessa variabler och de tre fågelarterna föreligger också starka negativa, statistiskt signifikanta samband. Slutsatsen från de båda undersökningarna, den i Tåkern och denna i Krankesjön, blir att en grund slättsjös kvalitet som ruggnings- och rastningslokal för simfåglar beror på tillgången på undervattensvegetation, vilken i sin tur hänger samman med algförekomst och siktdjup.

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Differences in foraging ecology of Wood Sandpiper *Tringa glareola* and Ruff *Philomachus pugnax* during spring migration in Sajna River valley (northern Poland)

Skillnader i födosöksekologi hos grönbena Tringa glareola *och brushane* Philomachus pugnax *under vårflyttningen i Sajnaflodens dalgång (norra Polen)*

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Abstract

The research was conducted in 2002, in Sajna River valley (NE Poland). It was aimed at foraging ecology of two wader species not specialised in terms of feeding techniques. We found that while foraging on a stopover site during spring migration Ruffs used different ecological niche than Wood Sandpipers. Ruffs foraged significantly more often in medium and deep water and made also more medium and deep probes, what indicates preference in random probing. High intensity and proportionally low efficiency of foraging may confirm it. Contrary, Wood Sandpiper foraged less intensively but much more effectively; this, together with frequent changes of feeding places in terms of water level indicate that Wood Sandpiper to greater extent uses visual detection of prey than Ruff.

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Introduction

Foraging waders use in general two basic techniques: visual detection of prey items and random probing of a substrate. The first one is used mostly by short-billed species e.g. plovers (*Charadrius* sp. and *Pluvialis* sp.). Long-billed waders such as godwits *Limosa* sp., curlews *Numenius* sp., Greenshank *Tringa nebularia* or Curlew Sandpiper *Calidris ferruginea* prefer the second method (Pienkowski 1982, Schnieder 1983, Piersma 1994). According to Durell (2000) Ruff *Philomachus pugnax* and Wood Sandpiper *Tringa glareola*, having relatively small eyes and medium-long bills, are among the not specialised species. The feeding technique that they choose depends on age or sex and also on local conditions on a feeding ground, i.e. substrate type, prey composition and availability, time of the day, and weather conditions (Goss-Custard 1969, Dugan 1982, Esselnik & Zwarts 1989, Wiersma & Piersma 1994, Skakuj 1999). Studies on bill anatomy of waders have revealed that there is a slight difference; Wood Sandpiper is to greater extent than Ruff, but also than closely related species, e.g. Redshank *Tringa totanus*, adapted to catching free-living and mobile organisms and therefore they rely more on visual detection of prey. The bill of the Ruff is more omni-potential as the species forages on a wider spectrum of food including plant material, particularly seeds (Hoerschelmann 1968, Cramp & Simmons 1983).

Spring migration of Ruff in northern Poland is rapid and starts in third decade of April with a peak in first decade of May (Meissner & Sikora 1995, Meissner & Włodarczak 1998, Wójcik et al. 1999); more easterly it starts earlier and proceeds longer – from beginning of April to mid-May (Górski & Nowakowski 1999), similar to the passage in southern Poland (Wiehle 1999). Wood Sandpipers are common on spring passage either inland or at the coast (Tomiałojć & Stawarczyk 2003) and are observed from second decade of April to mid-May (Meissner & Sikora 1995, Wójcik et al. 1999, Tomiałojć & Stawarczyk 2003). Both Ruffs and Wood Sandpipers migrate through Europe in a broad front, appearing only scarcely on coasts of northwestern Europe (Glutz von Blotzheim et al. 1975). Their stopover sites are inland wetlands, i.e. river valleys, muddy lake shores and wet grasslands. Despite their abundance during spring migration, inland-migrating waders were seldom a subject of foraging ecology research (van Roomen 2001).

The aim of this study is to characterise and compare foraging techniques of Ruff and Wood Sandpiper when stopping during spring migration in Sajna River valley in northeastern Poland (Varmia and Masuria District).

Materials and methods

The research was conducted from 29 April to 14 May 2002 near a field ringing station of Waterbird Research Group KULING. The study area covered Pleśno Reservoir and floodplains of Sajna River (N 54°04'; E 21°02', NE Poland) (Figure 1). Pleśno Reservoir (ca. 340 ha) was created by damming the floodplain between Sajna and Ryn rivers. Since 1998 it is protected by law as a land of ecological use (Nowicki & Cymes 2000). The lake is surrounded by dense vegetation, mainly reedbeds and rushes (*Phragmitetum comunis* and *Typhetum latifoliae* communities). Due to low water transparency, underwater vegetation is poorly developed and neophytes are dominants. The water level in the reservoir changes significantly during the course of the year, which makes it an attractive stopover site for migrating waders during spring and autumn (Meissner et al. 2002).

Observations of foraging birds were conducted from flood-dams by a telescope. Average distance was ca. 50 m, and this allowed us to avoid disturbance the birds' behaviour. Birds for observation were chosen randomly. From each bird 1-minute samples were collected. Maximally three samples were taken from each individual before switching to another bird. When 2 or 3 samples were taken from the same bird they were recalculated to one 1-minute sample. Large numbers of foraging birds and high turnover rate minimised the risk of double recordings of the same individual. The time spent by the birds on foraging, preening and alert activities was recorded with 1-second accuracy. Other activities were seen very seldom (e.g. aggressive behavior) or did not appear during observations at all (e.g. lekking (in Ruff) or flight). Number of attempts to catch a prey was recorded, distinguishing between whether or not it resulted in swallowing the prey. Observations were conducted only in daytime and they were split into 3.5-hour periods: 6:00–9:30 (morning), 9:30–13:00 (noon), 13:00–16:30 (afternoon) and 16:30–20:00 (evening).

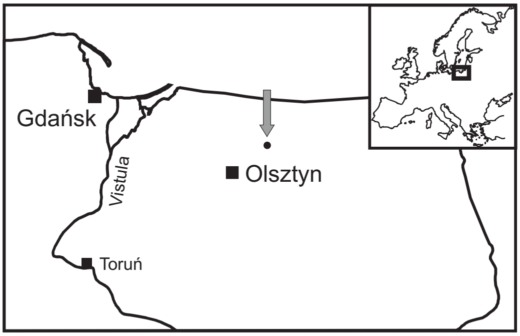

Figure 1. Location of the study area.
Platsen för undersökningsområdet.

The observed birds foraged on a muddy ground to various extent covered with water and plants. Three categories of water depth were distinguished: shallow (covering toes at most), medium (up to tarsus joint) and deep (over the tarsus joint). Also depth of bill submersion was classified into three categories: shallow (prey items collected from the ground or bill submerged up to its quarter length), medium (bill submerged up to nostrils) and deep (over the nostrils).

Intensity of foraging (I) was defined as the number of all probes in a minute, success of foraging (S) as the number of prey items caught in a minute, and efficiency of foraging (E) as the percentage of all probes that were successful (prey item caught) in a minute ($E=S/I*100$). Significance of differences between foraging in different levels of water and different depths of probes within species and sex was checked with Kruskal-Wallis test, while significance of differences between species and sexes was checked with Mann-Whitney test. Significance of differences between time budgets in succeeding day periods was tested using ANOVA test with Tukey post-hoc test (Zar 1996). All statistics were made in Statistica 6.0 software (StatSoft 2001).

Results

Comparison of feeding techniques of Ruff males and females

During the observations 424 samples for Ruff were recorded (27 for males and 397 for females). No differences between sexes were found in intensity, success and efficiency of foraging (Table 1).

Time budgets of males and females were compared (Table 2) and no significant differences were revealed in frequency of time spent on foraging and resting (Mann-Whitney test, $p<0.05$ in both cases). Males spent more time on alert than females (Mann-Whitney test, $Z=1.97$, $p<0.05$).

We analysed males' and females' frequency of probing in different water depths but neither here

Table 1. Median intensity, success and efficiency of foraging for males and females of Ruff. N=number of individuals studied.
Medianintensitet, framgång och effektivitet vid födosök hos hanar och honor av brushane, N=antal studerade individer.

Sex *Kön*	N	Intensity *Intensitet*	Success *Framgång*	Efficiency [%] *Effektivitet*
Females *Honor*	397	26	8	30,0
Males *Hanar*	27	25	7	29,4
U Test		Z=0.89, p=0.37	Z=1.15, p=0.25	Z=0.23, p=0.82

Table 2. Time budget of Ruff and Wood Sandpiper in Sajna river valley. N=number of individuals studied.
Tidsbudget för brushane och grönbena i Sajnaflodens dalgång. N=antal studerade indivier. F=hona, M=hane.

Species *Art*	Sex *Kön*	N	Foraging *Födosök*	Preening *Putsning*	Alert *Uppsikt*	Kruskal-Wallis test
Ruff *Brushane*	F	397	92.1%	7.7%	0.2%	H=914.97, p<0.001
Ruff *Brushane*	M	27	92.3%	6.8%	0.9%	H=69.19, p<0.001
Mann-Whitney test			Z=0.16, p=0.87	Z=0.79, p=0.43	Z=1.97, p=0.049	
Ruff *Brushane*	F+M	424	92.1%	7.6%	0.3%	H=982.50, p<0.001
Wood Sandpiper *Grönbena*		477	93.9%	5.8%	0.4%	H=1149.87, p<0.001
Mann-Whitney test			Z=3.73, p<0.05	Z=0.16, p<0.05	Z=0.39, p=0.70	

Table 3. Percentage distribution of probing of Ruff and Wood Sandpiper during foraging in different levels of water. N=number of probes. Mann-Whitney test in all cases: Z=0.00, p=1.00 and Kruskal-Wallis test in all cases: H=0.00, p=1.00.
Fördelningen av borrningar eller ytplock hos brushane och gröbena under födosök i olika vattendjup. N=totala antalet borrningar eller plock. F=hona. M=hane.

			Water depth *Vattendjup*		
Species *Art*	Sex *Kön*	N	Shallow *Grunt*	Medium *Medium*	Deep *Djupt*
Ruff *Brushane*	F	10167	3.7%	38.8%	57.5%
Ruff *Brushane*	M	632	0.0%	42.1%	57.9%
Ruff *Brushane*	F+M	10799	3.5%	39.0%	57.5%
Wood Sandpiper *Grönbena*	F+M	4674	7.9%	66.0%	26.1%

Table 4. Percentage distribution of probes of different depth in Ruff and Wood Sandpiper. N=number of probes. Mann-Whitney test in all cases: Z=0.00, p=1.00 and Kruskal-Wallis test in all cases: H=0.00, p=1.00.
Fördelningen av olika djupa nerstickningar av näbben hos brushane och grönbena. N=totala antalet nerstickningar av näbben. F=honor. M=hanar.

Species	Sex	N	Probing depth Nerstickningens djup		
Art	*Kön*		Shallow *Grunt*	Medium	Deep *Djupt*
Ruff *Brushane*	F	10167	4.5%	46.4%	49.0%
Ruff *Brushane*	M	632	0.0%	55.7%	44.3%
Ruff *Brushane*	F+M	10799	4.3%	47.0%	48.8%
Wood Sandpiper *Grönbena*	F+M	5136	62.2%	18.2%	19.6%

Table 5. Intensity and efficiency of foraging of Ruff and Wood Sandpiper during spring migration in Sajna river valley. Period of day (hours): 1 (6:00-9:30), 2 (9:30-13:00), 3 (13:00-16:30), 4 (16:30-20:00). N = number of individuals studied. Intensity – number of probes per 1 minute. Efficiency – percent of successful probes.
Intensitet och effektivitet i födosöket hos brushane och grönbena under vårflyttningen i Sajnafjodens dalgång under olika perioder av dagen: 1 (6:00–9:30), 2 (9:30–13:00), 3 (13:00–16:30), 4 (16:30–20:00).

Species *Art* Activity *Aktivitet*	Period	N	Mean *Medel*	SE	SD	Range *Intervall*	Differ from *Skilt från*
Ruff	1	98	22.9	0.8	7.5	0.0-52.0	2, 4
Intensity	2	132	26.3	0.8	8.6	0.0-45.0	1
Brushane	3	69	22.3	1.2	10.2	0.0-44.0	4
Intensitet	4	125	28.4	0.9	10.4	0.0-53.0	1, 3
Ruff	1	96	30.9	0.9	9.3	8.3-47.6	4
Efficiency (%)	2	129	32.8	0.7	7.9	0.0-52.4	4
Brushane	3	68	31.9	1.1	8.8	0.0-60.0	4
Effektivitet (%)	4	118	25.2	0.7	7.1	9.5-43.3	1, 2, 3
Wood Sandpiper	1	116	13.1	0.7	7.4	0.0-27.0	2
Intensity	2	175	8.2	0.5	6.2	0.0-31.0	1, 3, 4
Grönbena	3	104	11.1	0.6	5.9	0.0-24.0	2
Iintensitet	4	82	12.5	0.7	6.1	0.0-27.0	2
Wood Sandpiper	1	103	58.3	1.7	17.4	0.0-100.0	-
Efficiency (%)	2	155	62.1	1.7	21.5	0.0-100.0	-
Grönbena	3	100	65.2	1.9	18.8	0.0-100.0	-
Effektivitet (%)	4	79	61.7	2.0	17.6	33.3-100.0	-

we found any differences (Mann-Whitney test, Z=0.96, p=0.34). Both sexes made most of their probes in deep water (Table 3).

No significant difference between Ruff sexes was recorded while analysing bill immersion depths (Mann-Whitney test, Z=1.06, p=0.29). Preferences in bill immersion depths differed slightly between the sexes. Most often males made deep probes, but no shallow ones at all (Table 4).

Comparison of feeding techniques of Ruffs and Wood Sandpipers

During the observations 477 samples for Wood Sandpiper were obtained. Since we found no differences between sexes in the Ruff, the data for males and females were pooled. The median intensity of foraging of Ruffs was 26 probes/min and this was significantly higher than in Wood Sandpiper with only 11 probes/min (Mann-Whitney test, Z=20.75, p<0.001). Also median success of foraging of Ruffs (8 prey items/min) was significantly higher than of Wood Sandpipers (6 prey items/min) (Mann-Whitney test, Z=4.84, p<0.001), but mean efficiency of foraging was significantly lower in Ruff than in Wood Sandpiper (30.0% and 62.5%, respectively, (Mann-Whitney test, Z=-22.21, p<0.001). Both species spent most of the time on foraging – over 90% of a day (Table 2). Time budgets did not differ significantly between species (Mann-Whitney test, p>0.05 in all cases).

Time budget in succeeding day periods was compared. Because alert activity was not always recorded or it gained very low values, only distributions of two activities (foraging and preening) were checked. No significant changes in time budget were recorded, neither for Ruff nor for Wood Sandpiper (Mann-Whitney test, in all cases p>0.05). No differences were either found in comparison of particular day periods between species (Mann-Whitney test, in all cases p>0.05).

Intensity (ANOVA, $F_{3,424}$=9.71, p<0,001), success (ANOVA, $F_{3,424}$=7.31, p<0,001) and efficiency (ANOVA, $F_{3,411}$=19.85, p<0,001) of foraging differed between day periods in Ruff. Intensity of foraging of this species was lowest in the morning and in the afternoon, and highest in the evening, but success of foraging reached highest values at noon. The Ruffs' efficiency of foraging was lowest in the evening (Table 5). In Wood Sandpipers there were significant differences in the intensity (ANOVA, $F_{3,477}$=40.95, p<0,001) and success (ANOVA, $F_{3,477}$=17.10, p<0,001) of foraging between day periods, as well. Wood Sandpipers foraged less intensively at noon and they had then the lowest success. Efficiency of foraging of Wood Sandpipers did not differ between day periods (ANOVA, $F_{3,437}$=2.14, p=0,09) (Table 5).

Due to the foraging technique of the Wood Sandpiper, it was not possible to compare objectively time budgets of birds foraging in different water levels. During 56.5% of the one-minute observations (N=437) Wood Sandpipers changed the depth of water and foraged in at least two water levels. Some of the changes were so rapid that it was not possible to record the time birds foraged in water of a given depth. Therefore frequencies of probing of Ruffs and Wood Sandpipers in different water levels were compared and significant differences were revealed (Mann-Whitney test, Z=35.95, p<0.001). Ruffs made most probes in deep water while Wood Sandpipers made them in water of medium depth (Table 3). Significant differences were found also in depth of probes (Mann-Whitney test, Z=106.35, p<0.001). Ruffs made mostly medium and deep probes, but Wood Sandpipers made mainly shallow ones (62.2%, N=5136) (Table 4). Moreover, 40.3% of the Wood Sandpipers' shallow probes were actually surface pecks, i.e. collecting prey items from water surface and floating leaves.

Discussion

Efficiency of foraging of the Ruff in Sajna river valley reached 30% and was only half of the value found in Wood Sandpiper, while intensity of foraging showed the converse pattern – Ruffs foraged twice as intensively as Wood Sandpipers. The foraging behaviour of the Ruff was typical for species using random probing. They foraged mostly in deep water making predominantly deep probes, often submerging the whole head which surely makes visual detection of prey impossible. Wood Sandpipers, on the other hand, foraged in medium water with mainly shallow and surface probes. Low intensity of foraging linked with its high efficiency indicates visual detection of prey. Another confirmation is that Wood Sandpipers sometimes changed their foraging technique – they stopped probing in shallow or medium water and ran up directly to prey items seen up to one meter away. Such habits has been previously found in Greenshank (van Roomen 1998, Ntiaoma-Baidu et al. 1998).

High frequencies of deep probes in Ruff and shallow probes in Wood Sandpiper suggest partial segregation of foraging niches, at least in places where they occur together. Ruffs, thanks to longer legs and bill could also choose foraging in deeper water, inaccessible for Wood Sandpipers. Whereas the latter ones often fed on floating platforms of neophytes, which was also found in this species at Akyatan Gölü lake, Turkey (Dijksen & Kivit 1994), those floating plants were not accessible for the heavier Ruffs.

Foraging was the major activity in the time budget of the Sajna river birds. Similar results were found for Ruffs stopping in Cukurova seashore in Turkey where they spent 99% of daytime on foraging in April and 93% in May (Hannewijk 1994). Such predominance of foraging in spring migration reflects the necessity of gaining sufficient energy reserves in short time, which allows the birds to reach breeding grounds as fast as possible. In Münster (Germany) on the turn of April Ruff males spent most time on foraging before noon, while females did so in the afternoon. In both sexes a decrease of time spent on foraging was found in the evening (Melter 1995). A similar pattern was recorded in our study. However, in this part of the day Ruffs foraged with highest intensity but with lowest efficiency. This may be linked with changes in vertical distribution of invertebrates. Together with fall of temperature potential prey may move down in the substrate, which makes catching more difficult (Kalejta 1992). The significance of temperature drop on prey accessibility – and its consequence on feeding ecology – was proven for Redshanks wintering in Great Britain. In colder days the birds were forced to forage in deeper water, which was caused by lower accessibility of prey in shallower water (Goss-Custard 1969).

The Ruffs reached high efficiency of foraging around noon (9:30–13:00), when also intensity was very high – close to the level recorded in the evening. This suggests that the noon hours is the most important period of a day for gaining energy reserves during stopover in Sajna river valley. In Wood Sandpipers foraging efficiency in the evening was at the same level as in the rest of the day. At the same time birds foraged least intensively so they most probably used visual detection of prey.

During our study nocturnal observations were not practised although morning intensification of foraging together with the fact that birds did not enter walk-in traps nor mist nets during nights may prove that Wood Sandpipers did not forage at night or made it very seldom. In a closely related species – Green Sandpiper *Tringa ochropus* – nocturnal foraging was not recorded (Smith et al. 1999). On the other hand, Ntiaoma-Baidu et al. (1998) observed a few Wood Sandpipers (as well as other *Tringa* species) foraging at night at tropical wintering sites. Also Redshanks wintering in the temperate zone were found undertaking nocturnal foraging in bad weather conditions and with low accessibility of prey (Goss-Custard 1969). Low morning foraging intensity of the Ruff in our study may indicate that this species forages at night as was the case in the Lapwing *Vanellus vanellus* (Milsom et al. 1990).

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Sammanfattning

Födosökande vadare använder två olika metoder för att upptäcka bytena. Synen används främst av kortnäbbade arter såsom pipare. Långnäbbade arter, exempelvis spovar, gluttsnäppa och spovsnäppa, söker hellre föda genom att slumpvis borra med näbben i substratet. Brushane och grönbena, som har ganska små ögon och medellånga näbbar, är inte särskilt specialiserade och vilken teknik de väljer beror på ålder, kön och lokala förhållanden (substratet, typ av byten och deras tillgänglighet, tid på dygnet, väder). Under den snabba vårflyttningen rastar brushane och grönbena på inlandslokaler, där de söker föda på dyiga stränder och blöta gräsmarker. Denna studie syftar till att jämföra födosökstekniken hos grönbena och brushane, och studien utfördes i Sajnaflodens dalgång i nordöstra Polen mellan 29 april och 14 maj 2002. Varierande vattenstånd och ringa vegetation innebär att platsen är attraktiv för rastande vadare både vår och höst.

Slumpvis valda individer studerades med tubkikare på ungefär 50 m avstånd. Varje vald individ studerades under portioner om en minut, maximalt tre minuter. I de fall som en individ observerades under mer än en minut, räknades värdena om till en minut och varje sådan minut utgör således ett stickprov. Tre typer av aktiviteter registrerades med en sekunds noggrannhet: födosök, fjädervård och vakthållning (i praktiken dock bara de två förstnämnda eftersom vakthållning noterades sällan). Antalet födosöksförsök registrerades och vi skiljde på lyckade (byte togs) och misslyckade. Observationerna gjordes endast under dagtid och vi delade upp dagen i fyra 3,5-timmarsperioder mellan klockan 06.00 och 20.00.

Fåglarna sökte föda på gyttja och låg vegetation som delvis var täckt av vatten av varierande djup. Vi registrerade om födosöket skedde på grunt (vattnet högst över tårna), medeldjupt (upp till tarsleden) och djupt vatten. Hur djupt näbben fördes ner registrerades också i tre klasser: grunt (plockade på marken eller förde ner näbben till högst en fjärdedel), medel (upp till näsborrarna) och djupt. Födosöksintensiteten definierades som antalet försök per minut, framgången som antalet byten tagna per minut och effektiviteten som procenten lyckade försök av samtliga.

Totalt insamlades 424 stickprov för brushane (27 från hanar och 397 från honor). Inga skillnader fanns mellan könen (Tabell 1–4), varför könen slogs ihop vid jämförelsen med grönbena. För grönbena registrerades 477 stickprov. Brushanarna födosökte med signifikant högre intensitet än grönbenorna (26 resp. 11 försök per minut). Framgången, antalet byten per minut, var också signifikant högre, 8 för brushane mot 6 för grönbena. Däremot var effektiviteten lägre hos brushanen (30%) än hos grönbenan (62,5%). Fördelningen mellan olika aktiviteter var densamma hos båda arterna och mer än 90% av tiden ägnades åt födosök. Hos brushanen fanns det skillnader i intensitet, framgång och effektivitet i födosöket mellan olika perioder av dagen medan det hos grönbenan var skillnader enbart för intensitet och framgång. Brushanen födosökte mestadels i djupt, medan grönbenan föredrädesvis födosökte i medeldjupt vatten (Tabell 3). Brushanen förde oftast ner näbben medeldjupt eller djupt, medan grönbenan till stor del plockade från ytan eller från flytande blad.

Våra observationer visar att brushanens födosök var typiskt för arter som slumpvis söker föda genom att borra ner näbben i substratet, ofta i kombination med att huvudet sänktes ner i vattnet, något som utesluter att de använde synen. Grönbenorna plockade ytligt och deras låga sökintensitet i kombination med hög framgång indikerar att de använde synen. Skillnaderna visar att de två arterna exploaterar olika födonischer.

Att födosök är den huvudsakliga aktiviteten när brushanar och grönbenor rastar under vårflyttningen tycks vara regel, och har noterats i andra studier också. Förklaringen till detta är naturligtvis att de måste samla energi snabbt så att de kan nå häckningsområdet så fort som möjligt. Vi gjorde inga observationer nattetid. Men frånvaron av fångade grönbenor i vadarburar och slöjnät under natten indikerar att de inte sökte föda då, vilket är väntat om de främst använder synen. Hur det var med brushanen vet vi inte, men den låga fördosöksintensitet som vi noterade på morgonen kan vara en indikation på att de sökte föda nattetid, vilket bör vara möjligt för en art som söker med näbben nere i substratet.

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First, second and replacement broods in the breeding biology of a Treecreeper *Certhia familiaris* population

Förstakullar, andrakullar och omläggningskullar i häckningsbiologin hos en population trädkrypare Certhia familiaris

ANDERS ENEMAR

Abstract

The breeding behaviour of a Treecreeper population that bred in nest pockets and in which all females were colour-ringed was followed over ten seasons. On average, 50% of the first breeding attempts in spring failed. Between half and two thirds of the successful females were double-brooded. The remaining females were single-brooded. These two breeding categories were identical in terms of initial clutch size and egg volume. The double-brooded females invested less in their second than their first clutch. Most of the females that failed laid replacement clutches of similar size as in the first attempt but with larger eggs. A replacement brood where young successfully fledged was never followed by a second breeding attempt. The average distance between the first and the repeat nest was the same for double-brooded and replacement-breeding females. The egg volumes of the first and the repeat clutches were strongly correlated. The double-brooded pairs were the most common breeding category and reared 50% of the population's total output of fledged broods, while the single-brooded and replacement breeding pairs each fledged ca. 25%. The adaptive values of the three breeding categories are compared.

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Introduction

Many passerine bird species rear more than one brood per breeding season. In cases where they lay two or more clutches after having successfully fledged a first brood, they are said to be double or multi-brooded, respectively. If there is only one clutch, they remain single-brooded. Clutches laid to compensate for failed breeding attempts are often called replacement clutches or broods. The occurrence of multi-broodedness among birds has been analysed in relation to e.g. the quality of the parent birds, reproductive timing, seasonal pattern of clutch size variation, food abundance, migratory behaviour and regional location (e.g. Klomp 1970, Drent & Daan 1980, Crick et al. 1993, Svensson 1995, Verboven & Verhulst 1996, Farnsworth & Simons 2001, Dhondt et al. 2002, Weggler 2006, Siefferman & Hill 2008). The subject of this study, the Treecreeper *Certhia familiaris*, is a resident and insectivorous small passerine that starts breeding in early spring. These characteristics suggest that the Treecreeper should be more or less frequently double-brooded and exhibit an intra-seasonal clutch size variation with a mid-season peak, and earlier studies have confirmed this (Kuitunen 1987, Enemar 1992, Crick et al. 1993).

The aim of the present study is to describe the breeding course of a Treecreeper population with regard to the frequency and significance of the different categories of reared broods. This requires a comparison between the first, second and replacement broods, primarily with regard to the frequency, number and size of eggs, timing of laying and length of distance from the nest site of the first brood to that of the second or replacement broods. Unfortunately, reliable data on fledging success are not available for the later part of the breeding seasons. Nor has the abundance of food in the habitats been investigated. As replacement clutches have been identified in the present study females that lay these clutches are designated "replacement-breeding" and comprise the failed presumptive single and double-brooded females. The replacement-breeding pairs constitute an important part of the studied breeding population.

Methods

The data of the present study were collected between 1995 and 2005, i.e. ten seasons excluding the 2004 season, in a study area of about 2.5 km^2, mainly located in the Gunnebo recreation grounds near Göteborg (57° 39´ N; 12° 4´ E). The area is mainly covered by deciduous broad-leaved forests and contains 200 nest-boxes for Treecreepers, so-called nest pockets. They were made of pieces of roofing felt and attached to the tree trunks with a mean distance of 75 m between them (Enemar 1992). A piece of aluminium sheet was attached to the occupied nest pockets to prevent the Great Spotted Woodpeckers *Dendrocopos major* from penetrating the pocket wall to rob the nest. The density of pockets was sufficiently high to permit the Treecreeper pairs to easily find another pocket for the repeat nests. The pockets were inspected at various intervals depending on the demands of the season's research program, but always frequently enough to establish the number and character of the clutches.

Most breeding females were caught and colour-ringed when incubating complete clutches. They were forced to leave the nest-pocket and captured in a plastic bag at the opening, after which they were provided with unique combinations of one metal and three coloured rings for identification of individuals and confirmation of second or replacement broods.

The length of the breeding season of the double-brooded and replacement-breeding Treecreepers was counted from the start of laying the first clutch to the fledging of the repeat brood. The distance between the two nest-pockets used by the re-nesting females was measured on maps with a scale of 1:10,000.

The daily mean temperatures were obtained from Säve airport (SMHI 1995–2005), about 15 km to the north of the study area. These temperatures are closely correlated to those of the study area (r = 0.98; Enemar 1997). The mean ambient temperature during laying of a clutch was calculated using the mean daily temperatures during the period from one day before the first laid egg to the day before the last egg.

The egg lengths and breadths were measured to the nearest 0.05 mm on enlarged prints of photographed clutches using a sliding calliper (Enemar 1997, 1999). The volumes were calculated in accordance with Hoyt (1979). The measurements by Enemar (1997) were used when allowing for the effect of the varying clutch size on egg volumes. In order to control for the effect of ambient temperature variation, the previously established correlation between the temperature and the egg volumes of the first clutches in April was applied (r = 0.49, b = 0.19) (Enemar 1997). This relation is almost the same for the repeat clutches laid in May and early June (r = 0.34, b = 0.11, calculated for this study).

The statistical methods used were the Chi square test, G-test, Mann-Whitney U-test, correlation and regression, two-sample t-test, t-test for matched pairs and one-way ANOVA, mainly in accordance with Fowler & Cohen (no printing year). The variability is given as standard deviation.

Results

The total number of laid first clutches and the frequency of second and replacement clutches can be found in Table 1.The frequency of replacement clutches (71% of the females that failed in their first brood) significantly exceeds that of second clutches (51% of the females that had a successful first brood) (G_{adj}=5.12, p< 0.05). As no second clutches were laid in 1996 due to the fact that all first broods failed, that year should be excluded from the comparative test, which increases the frequency of the replacement clutches to 76% and the difference between the two repeat clutch categories by five percentage units (G_{adj}=7.07, p< 0.01). However, no less than 43 out of the 118 first clutches were laid by females that stayed in or returned to the study area for one to three seasons after surviving the winter. Including each female only once in the analysis (to avoid pseudoreplication) reduces the number of studied females to 75. Their breeding behaviour was only considered in the season during which they were ringed. They produced 42 successful and 33 failed first broods. Despite this reduction in sample size (not applied to the remaining analyses in the present study), the frequency of laid replacement clutches (79%) still significantly outnumbers that of the second clutches (57%) (G_{adj}=3.91, p< 0.05). The conclusion is that failed breeders produced replacement clutches at a higher rate than successful first breeders produced second clutches.

The annual figures for the three breeding categories are presented in Table 1. The number of second and replacement clutches represents the number of double-brooded and replacement-breeding Treecreepers, respectively. The number of single-

Table 1. Number and frequency of the different categories of clutches among 118 Treecreeper pairs that started laying their first clutches in the nest pockets within three weeks after the appearance of the season's first egg. The percentage values of the second and replacement clutches indicate the shares of successful and failed first clutches, respectively.
Antal och procentuella andelar av de olika slagen av kullar hos 118 trädkryparpar som började värpa förstakullen inom tre veckor efter säsongens första ägg. Procenttalen för andrakullarna och omläggningarna är beräknade på antalet lyckade resp. förlorade förstakullar.

	First clutches *Förstakullar*			Repeat clutches *Förnyade kullar*			
Year *År*	Number laid *Antal värpta*	Successful *Lyckade*	Failed *Förlorade*	Second clutches *Andrakullar*	Replacement *Omläggningar*	None * *Inga*	Unknown** *Okända*
1995	16	7 (44%)	9 (56%)	5 (71%)	8 (89%)	2 (29%)	1
1996	13	0 (0%)	13 (100%)	0 (0%)	7 (53%)	0 (0%)	6
1997	12	5 (42%)	7 (58%)	5 (100%)	6 (86%)	0 (0%)	1
1998	11	7 (64%)	4 (36%)	5 (71%)	4 (100%)	2 (29%)	0
1999	15	10 (67%)	5 (33%)	4 (40%)	4 (80%)	6 (60%)	1
2000	11	8 (73%)	3 (27%)	4 (50%)	2 (67%)	4 (50%)	1
2001	11	5 (45%)	6 (55%)	2 (40%)	4 (67%)	3 (60%)	2
2002	4	2 (50%)	2 (50%)	0 (0%)	2 (100%)	2 (100%)	0
2003	11	4 (36%)	7 (64%)	1 (25%)	4 (57%)	3 (75%)	3
2005	14	11 (79%)	3 (21%)	4 (36%)	1 (33%)	7 (64%)	2
Totals	118	59 (50%)	59 (50%)	30 (51%)	42 (71%)	29 (49%)	17

*) The figures also represent the number and frequency of single-brooded pairs.
Siffrorna anger även antal och procentuell andel enkullhonor.
**) The figures represent the number of females that disappeared after the failed first brood.
Siffrorna anger antal försvunna honor efter misslyckad förstakull.

brooded pairs is presented in the second last column of Table 1 ("None").

The time schedule of the double-brooded and replacement-brooded females is presented in Table 2. The laying of the replacement clutches started about two weeks before the second clutches, thus there is a significant difference between the median dates (Mann-Whitney, U=29, $p < 0.05$). It took about two days less to fledge the second broods compared to the replacement broods, also a significant difference ($F_{1,28} = 8.39$, $p < 0.01$). The double-brooded females needed about one week longer to fledge two broods than the replacement-brooded females to fledge one, a small yet significant difference (Mann-Whitney, U = 26, $p < 0.05$). The median date (relative value counted from the first egg of the season) of the laying start of 25 single-brooded females tended to be one day later than that of 31 double-brooded females (t=1.69, $0.2>p>0.1$). The tendency was the same although increased to two days as regards the fledging dates of 28 single-brooded females and 30 double-brooded females (t=1.91, $0.10>p>0.05$). According to data from six breeding seasons (Table 2), the mean nesting periods of a total of 15 successful double-brooded females are 37.8 days and 34.5 days for the first and second brood, respectively, a significant difference of 3.3 ± 2.5 days (matched pairs t = 5.077, df=14, $p<0.001$). The mean temperature during the nesting periods of the two brood categories increased significantly from 10.4±1.3 °C to 14.0±1.1 °C ($F_{1,29} = 6.32$, $p<0.05$). The durations of the first nesting periods are not correlated with temperature means, whereas those of the second broods indicate a negative relationship ($r^2 = 0.22$, df = 13, $0.1> p>0.05$).

The females moved a mean distance of 146±90 m (n=32) and 166±110 m (n=40) to lay their second and replacement clutches, respectively. The difference between the means is not statistically significant (t = 0.849, df = 70, $0.4>p>0.3$).

The variation in clutch size during the progress of the breeding season is presented in Table 3. The laying season starts and ends with small clutches belonging to the first and second broods, with peak size in the middle of the season mainly consisting of replacement clutches. The 36 females that fledged a first brood (mean clutch 5.51±0.56) laid second clutches with fewer eggs (5.22±0.72),

Table 2. Time schedule of the breeding process of 30 female Treecreepers that laid either second or replacement clutches. The failed first clutches were deserted mainly due to trapping and colour ringing, heavy rain, or robbing. The figures in brackets below the median dates indicate the earliest and latest first-eggs. The interval between broods is counted from the fledging or desertion day of the first clutch to the day on which the laying of the repeat clutch was started.
Häckningens tidsförlopp för 30 trädkryparhonor som värpte antingen en andrakull eller en ersättningskull. De misslyckade förstakullarna övergavs som följd av fångst och ringmärkning, ymnigt regnande eller borövning. Siffrorna inom parentes under varje mediandatum anger datum för det tidigaste och senaste första-ägget. Antal dagar mellan kullarna räknas från förstakullens utflygning till nästa kulls värpstart.

	First brood *Första kullen*				Repeat brood *Nästa kull*		
	Number of females *Antal honor*	Median date of 1st egg *Median-datum 1:a ägg*	No. of days from 1st egg to fledging or nest desertion *Botid från 1:a ägg till utflygning/övergivning*	Days between broods *Dagar mellan kullarna*	Median date of 1st egg *Median-datum för 1:a ägg*	Days from 1st egg to fledging *Botid från 1:a ägg till utflygning*	Length of breeding period *Häckningstidens längd*
Successful first and second brood *Lyckad första- och andrakull*	15	23 April (15/4–2/5)	37.8±1.8	2.5±2.1	2 June (19/5–13/6)	34.5±1.1	74.9±3.2
Failed first and successful replacement brood *Misslyckad förstakull och lyckad omläggning*	15	20 April (10/4–3/5)	20.8±7.2	9.5±3.9	19 May (7/5–5/6)	36.8±1.9	67.1±6.5

Table 3. The mean sizes (+S.D.) of the first, second, and replacement clutches from the seasons 1995–2005, distributed across ten- or eleven-day periods from the start of laying. n = number of clutches.
Medelstorleken på första- och andrakullarna samt omläggningarna från säsongerna 1995–2005, fördelade på de tio- eller elva-dagarsperioder då första ägget värptes. n = antal kullar.

Clutch	April		May			June		April–
Kull	11–20	21–30	1–10	11–20	21–31	1–10	11–20	June
First	5.52	5.68	5.88	6	6	–	–	5.66
Första	±0.59	±0.53	±0.64					±0.56
n	24	40	8	1	1	–	–	74
Second	–	–	–	5	5.55	5.09	5	5.22
Andra					±0.82	±0.68		±0.72
n	–	–	–	1	11	22	2	36
Replacem.	–	–	6	6.25	5.52	4.83	5	5.63
Omläggn.				±0.45	±0.77	±0.75		±0.82
n	–	–	1	11	19	6	1	38
All	5.52	5.68	5.89	6.15	5.55	5.04	5	5.55
Alla	±0.59	±0.53	±0.60	±0.55	±0.77	±0.69		±0.69
n	24	40	9	13	31	28	3	148

Table 4. The mean egg volumes of the first and repeat clutches of 24 and 30 treecreeper females that started second and replacement broods, respectively. /*corr*. indicates that the volume has been corrected for the difference in clutch size and environmental temperature.
*Äggens medelvolym hos förstakullarna samt de därpå följande andrakullarna för 24 trädkryparhonor och. omläggningskullarna för 30 honor. /*korr. *anger att den del av volymändringen som beror på skillnaden i kullstorlek och omgivningstemperatur har dragits ifrån.*

Number of broods *Antal kullar*	Clutch *Kull*	Mean egg volume, cm^3 *Äggens medelvolym, cm^3*	Change from first to repeat clutch *Skillnad mellan kullar*	Matched pairs t-test of difference *Parvis test på skillnaden*	
				t	p
	Second *Andra*	1.17±0.07			
24			+0.018±0.047	0.502	>0.6
success-	First *Första*	1.15±0.07			
ful			+0.035±0.054	4.511	<0.001
lyckade	Second/*corr.* *Andra*/korr.	1.12±0.09			
	Replacement				
30	*Omläggning*	1.19±0.08			
failed			+0.031±0.031	3.134	<0.01
miss-	First *Första*	1.16±0.08			
lyckade			+0.010±0.024	2.209	<0.05
	Replacement/*corr.* *Omläggning*/korr.	1.17±0.11			

a small but statistically significant reduction (matched pairs t=2.16, df =35, p<0.05). The first (5.76±0.54) and repeat clutches (5.63±0.81) of 38 replacement-breeding females did not differ in size (matched pairs t=0.75, 0.5>p>0.4). The replacement clutches were larger than the second clutches (t=2.29, p<0.05). The mean size of the first clutches of 32 double-brooded females (5.6±0.62) did not differ significantly from that of 23 single-brooded females (5.8±0.47) (t = 1.360, p>0.1). Both samples emanated from the same eight seasons and only clutches laid within the three weeks after the appearance of the season's first egg were included.

The clutch means of the egg volumes are known for 24 double-brooded females (Table 4). The volumes of the first and second clutches of each individual female are strongly correlated (Figure 1). The small increase in the mean volumes from 1.15 cm^3 to 1.17 cm^3 is not significant ($F_{1,46}$ = 1.29, p>0.2), nor did the individual females lay significantly larger second clutch eggs (matched pairs t-test, Table 4). On the contrary, they laid on average significantly smaller second clutch eggs after controlling for differences in clutch size and mean ambient temperature during the laying period (Table 4).

The mean egg volumes of 16 single-brooded females (1.13±0.079 cm^3) do not differ from those of the first clutches of the double-brooded females in Table 4 ($F_{1,38}$= 0.49, p>0.2).

The mean egg volumes of 30 replacement clutches are strongly correlated to the means of the preceding first clutches (Figure 1). The mean egg size of the replacement clutches does not differ from that of the failed first clutches ($F_{1,58}$ = 3.40, 0.1>p>0.05) although the individual females laid on average significantly larger replacement eggs (Table 4). A minor increase remains, even after the effect of the differences in clutch size and temperature during laying has been subtracted from the egg volumes (Table 4).

Discussion

The frequency of the three brood categories

Classification of successful and failed first broods in the nest pockets requires knowledge of the presence as well as the absence of repeat breeding. The problem is that some repeat clutches may be laid in nest sites other than the nest pockets within or outside the study area. Such suitable nest sites behind loosened bark and similar crevices are probably rather common in the study area. Moreover, there are indications that the Treecreepers prefer natural

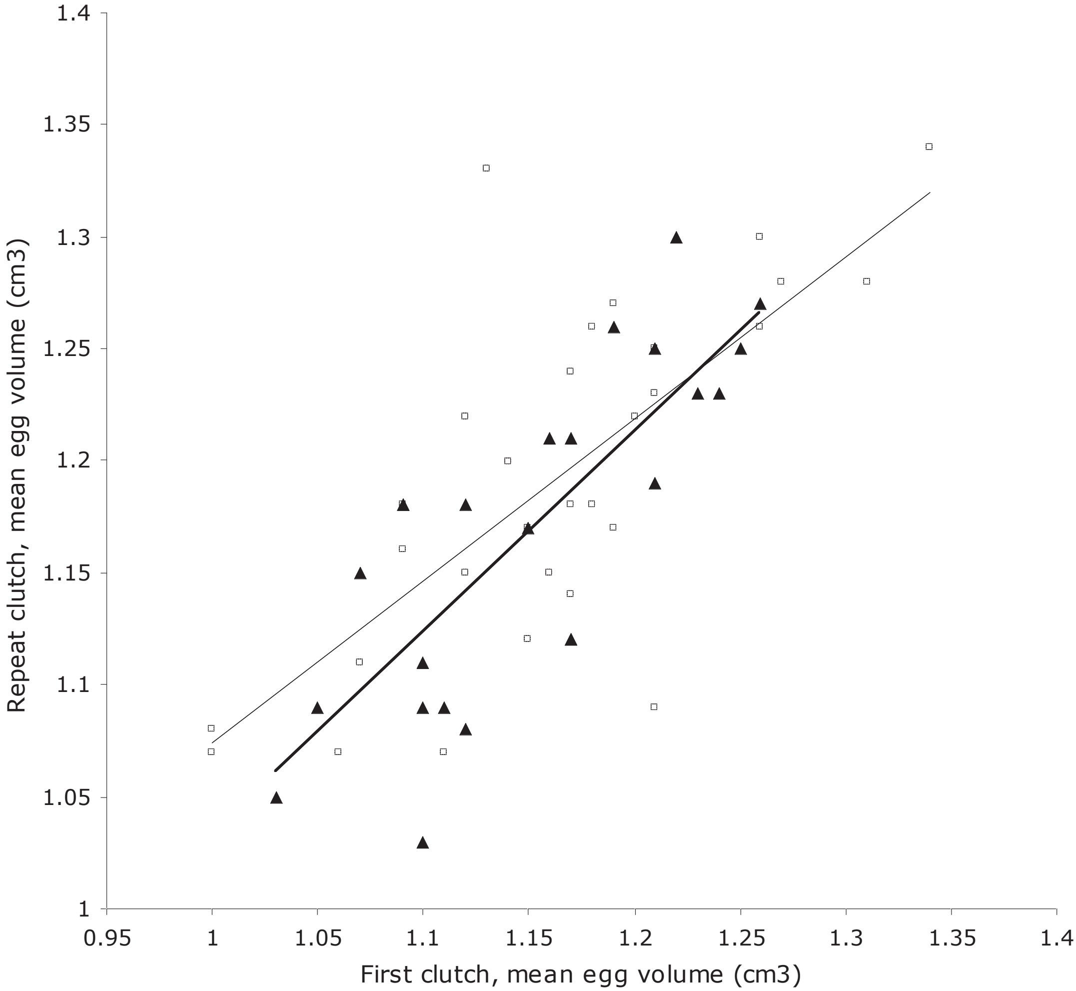

Figure 1. The correlation between the egg sizes (clutch means) within 24 pairs of first and second clutches (triangles, coarse regression line, $y = 0.89x + 0.14$, $r^2 = 0.62$, $p<0.001$) and within 30 pairs of first and replacement clutches (small open circles, thin regression line, $y = 0.72x + 0.35$, $r^2 = 0.54$, $p<0.001$).
Sambandet mellan äggstorlekarna (kullmedelvärden) inom 24 par av första- och andrakullar (tringlar, den grova linjen) och inom 30 par av förstakullar och omläggningskullar (små cirklar, den tunna linjen). Förstakullarnas äggvolymer kan avläsas på den horisontella axeln, andrakullarnas och omläggningskullarnas volymer på den vertikala axeln. De båda linjerna visar att då äggen i första kullen ökar i storlek så ökar också andra- och omläggningskullens äggstorlek. Sambanden är statistiskt säkerställda.

sites (Kuitunen & Aleknonis 1992). Unidentified repeat nests lead to an over-estimation of the number of single-brooded pairs and an under-estimation of the double-brooded and the replacement-breeding pairs. However, most of the double-brooded and replacement-breeding females in the population of the study area probably used the pockets for their repeat nests. This assumption is based on the following observations.

1. The Treecreeper females were extremely site tenacious, as only one out of 25 returning females was absent the season after colour ringing, but returned the following season.
2. The Treecreepers only moved fairly short distances within the study area between the first and the repeat breeding (see Results).
3. There was plenty of space available for re-breeding within the study area because its Treecreeper

population was sparse. The mean density was 5 ± 1.7 breeding pairs/km^2 (n=9), which corresponds to Treecreeper populations elsewhere (e.g. Steinfatt 1939, Kuitunen & Helle 1988, but see Schönfeld 1983, Schwerdtfeger 1987).
4. Each breeding pair had access to a surplus of unoccupied nest pockets within the territory.
5. During the field work in the study area, Treecreeper nests were never discovered in positions other than nest pockets.

Nevertheless, the numbers of repeat clutches accounted for in Table 1 most likely represent minimum values. New females without coloured rings that showed up every season in June and bred in the nest pockets might support this assumption. However, their number was small and represented a seasonal mean of three breeding females (3.0±1.7, n=9). Only once has a colour-ringed female from the preceding season appeared among these late newcomers. Obviously, female Treecreepers move into the study area (or have been overlooked when breeding in natural cavities there) in the middle of the breeding season to start second or replacement clutches. It is reasonable to assume that some Treecreepers may have crossed the study area border in the opposite direction, however probably fewer than the immigrants, because of the lack of nest pockets in surrounding areas. The average number of females that could not be found re-breeding in the study area after their first successful or failed brood is between four and five per year (4.6±2.5, n=10) as calculated on the basis of the last two columns of Table 1. Some may have started repeat clutches elsewhere, at a guess about the same number as the immigrating re-breeding females, i.e. three clutches equally divided into 1.5 second clutches and 1.5 replacement clutches per season. Adding these to the annual number of repeat clutches (Table 1) increases the number of second clutches to 43.5 (75%) (the exceptional year 1996 excluded), and the number of replacement clutches to 57.0 (97%).

These adjustments, although precarious, indicate that at least two thirds of the successful first broods were followed by a second breeding attempt, i.e. a doubled second brood frequency compared with those found in other Treecreeper populations (references below). It follows from the adjusted frequency of the double-brooded Treecreepers that about one third of the females were single-brooded. According to the adjusted values, practically all failed first broods were followed by replacement-breeding attempts.

The average rate of the second clutches as presented in Table 1 is rather high, 51%, when compared with the investigated nest-box populations in Finland (37%, Kuitunen 1987). A second clutch frequency of 32% was found in a Lithuanian population breeding in natural cavities (Kuitunen & Aleknonis 1992). The British nest card data indicate a rate of less than 20% (Flegg 1973). The percentage of the replacement broods also differs remarkably from those of the Finnish and Lithuanian populations (see below).

The high frequency of second broods occurring in the population of the study area is not unique, as it has been observed in another double-brooded small passerine, namely the likewise resident and forest-living Coal Tit *Parus ater* (Winkel & Winkel 1995).

The breeding season: time schedule and course of events

When comparing the time course and sequence of breeding events of the double-brooded and replacement-breeding females it is apparent that the latter normally managed to rear only one brood (Table 2). The start of a second clutch after a successful replacement brood has never been observed in the study area, and a replacement laying after a failed second brood has been noted only once in Finland by Kuitunen (1987). In order to rear two successive broods in the same season, the first clutch must obviously be laid in early spring and result in fledged young. A successful first brood started too late may preclude the laying of a second clutch (see below). Only once has a second brood followed a first brood started in May.

On average, the failed breeding was interrupted 17 days before the fledging day of the successful broods, a time span that was reduced to 14 days between the subsequent laying starts of replacement and second clutches (Table 2). Therefore the fledging of the replacement broods will be too late to make successful second brood rearing possible (see below).

The double-brooded female ensures time for the second brood by starting nest building (Kuitunen 1987, own observations) as well as oocyte growth and egg formation several days before the fledging of the first brood. The first egg of the second clutch was sometimes laid as soon as the day after the fledging day (mean interval 2.5 days, Table 2). The two broods were never observed to overlap. Elsewhere in Sweden, Durango (1963) found one breeding pair that had one nest with fledglings and one with eggs at the same time. Rare cases of overlapping have been reported from Germany and Finland (Bäsecke 1957, Kuitunen 1987). The absence of overlapping broods in the study area indicates that the normal food supply is not sufficiently rich to permit the female to lay eggs and feed young simultaneously (cf. Burley 1980).

The failed females started replacement laying in a new nest after one to two weeks (mean 9.5 days, Table 2) corresponding to the 6 to 12 days reported by Schönfeld (1983). The length of the interval may be at least partly dependent on the age of the first brood when destroyed. The lengths of the total breeding period of the double-brooded and replacement-brooding females differed significantly ($U=26$, $p<0.05$). The difference only amounts to approximately one week, as it takes longer to start laying a replacement clutch and fledge the young compared with the second brood (Table 2). The average fledging date of a replacement brood is around 25 June, which means that a hypothetical second brood would not fledge until about 1 August. Only two repeat broods fledged after 15 July. It is probably the advanced time of the season that somehow signals to the female to abstain from another breeding attempt when her replacement brood has fledged.

The distance between the nest site of the first and the repeat breeding

The nest-pocket of the first brood was never re-used in the same season. The distance between the two nests of the replacement-breeding female tended to be greater than that of the double-brooded female, although the difference was not significant (see Results). One third of both repeat clutch categories were laid in a pocket within 100 m of the first one. This means that the neighbouring empty pocket was used, as they were erected, on average, 75 m apart. As regards the double-brooded females, one would expect most of them to select a neighbouring pocket because the quality of the local habitat proved good enough to support successful breeding. Nevertheless, about one third (12 out of 32) of the females chose a more distant pocket, often ignoring unoccupied pockets in between. The reason might be that the food supply around the first nest site had been so depleted during the first brood rearing (cf. Jäntti et al. 2001) that it paid to move further away to the second nest site.

The same proportion (14 out of 40) of the failed females laid their replacement clutches beyond the nearest unoccupied pocket. Most of them lost their first brood more than one week prior to fledging, i.e. maybe before the food resources of the surrounding habitat were exploited heavily enough to necessitate a more distant move. Nevertheless, the double-brooded and replacement-breeding female Treecreepers did not differ significantly when selecting a nest pocket in order to start repeat breeding (see Results).

Clutch size

The clutch size variation during the breeding season illustrates the well known “calendar curve” in the Treecreeper (Kuitunen 1987, Enemar 1992). It peaked in the middle of the laying season, i.e. during the second ten days of May, when replacement laying has started (Table 3). The second clutches had significantly fewer eggs than the first clutches, which is in accordance with the “calendar curve” but may also be a consequence of the reduced egg-producing capacity of the females after having successfully reared a first brood.

Most replacement clutches are laid in the last 11-day period of May, when the peak-sized clutches of the preceding 10-day period have already started to decline and become similar to the size of the first appearing second clutches (Table 3). The mean size of all replacement clutches equals that of the preceding first clutches.

More detailed comparisons with Kuitunen’s (1987) results as regards Treecreeper clutch size have been made by Enemar (1992).

Egg-size

The double-brooded females laid approximately equal-sized eggs throughout the breeding season, although the second clutch eggs tended to be larger (Table 4). However, adjusting for the size-promoting effects of fewer eggs in the second clutch and the prevailing higher temperature during the egg formation period unveils a considerable reduction of the egg volumes. The latter may be a consequence of the weakened egg formation capacity of the female after rearing the first brood. This drawback may be compensated for not only by the somewhat reduced clutch size and the increased ambient temperature in June, but also by the longer days with a more favourable feeding situation in June (Kuitunen & Suhonen 1991).

The replacement-brooding females laid larger eggs in the repeat clutch than in the first failed one (Table 4). A significant minor size increase remains even after controlling for more favourable temperature during the replacement laying. The replacement-breeding females probably had a better physical condition than the double-brooded females, as they had on average invested in only part of what was required to fledge a first brood and they also waited ca. 7 days longer before starting the repeat brood (Table 2). The average temperature change between the laying periods of the first and the repeat clutch was of minor or no importance, as in both cases the interval is the same, increasing from +8°C to +13°C between the first and second clutches and from +7°C to +12°C between the first and replacement clutches.

The fitness gains, if any, related to the slightly larger replacement eggs are hard to judge. It is, however, a general rule among the small passerine species that larger eggs give rise to heavier hatchlings, although the lifetime fitness value of this relationship has not been sufficiently investigated (Williams 1994, Christians 2002, and see below).

The resident Great Tits *Parus major* in northern Finland (Ojanen et al. 1979) and Switzerland (Nager & Zandt 1994) exhibit much the same variation as the Treecreeper with regard to egg size in the different clutch categories. The replacement-brooding female lays significantly larger eggs in the repeat clutch (Ojanen et al. 1979) representing an increase of 3.2%. The corresponding percentage is 2.6% in the Treecreeper. Ojanen et al. also established high heritability of the egg dimensions of the first and second clutches. As indicated by the regression lines (Figure 1), heritable factors may also affect egg size in the Treecreeper. Females that laid small eggs in the first clutch generally did the same in the repeat clutch, and large first clutch eggs were followed by large repeat eggs, a highly significant correlation in both double-brooded and replacement-breeding Treecreepers.

To lay or not to lay a repeat clutch?

This question does not seem to be of immediate interest in a frequently double-brooded species such as the Treecreeper, especially as it has been demonstrated in other multi-brooded species that reproductive success is more a function of the number of reared broods than of e.g. clutch size (e.g. Smith & Roff 1980, Holmes et al. 1992, Soler et al. 1995, Winkel & Winkel 1995, Palomino et al. 1999). It is reasonable to assume, therefore, that all Treecreepers are hereditarily double-brooded although with a varying readiness to lay a second clutch. The females may differ in their sensibility to external or internal factors that inhibit a second breeding attempt. In any case and according to the interpretations above, about a third of the Treecreeper pairs do not seem to make a second breeding attempt and remain single-brooded when the first brood has fledged. The conditions and adaptive value of the two breeding strategies will be considered in the following. The replacement breeding will also be treated, as it is so frequent in the Treecreeper and, furthermore, because this breeding category, according to Roonem & Robertson (1997), has rarely been described in detail (but see e.g. Einloft-Aschenbach & Schmidt 1984).

The double-brooded female

Females that have fledged the first brood have to decide whether or not to invest in a second clutch. They have already fledged one brood, an achievement that probably took a considerable toll on their physical condition. Consequently, they invest less when producing the second clutch compared with the first one (Table 3 and 4). Rearing a second brood may further negatively affect their physical status, involving reduced prospects of surviving the subsequent winter as demonstrated in other small passerine species (e.g. Askenmo 1979, Bryant 1979, Verhulst 1998, but see Einloft-Achenbach & Schmidt 1984, Smith & Marquiss 1995, Winkel & Winkel 1995, Hario 1997). The delayed onset of moult following double-brooding may have important consequences for winter survival, at least in a long-distant migrant (Evans Ogden & Stutchbury 1996). Furthermore, the male Treecreeper participates only sporadically or not at all in feeding the second brood (Kuitunen et al. 1996, own studies), which further increases the rearing load on the female. Nevertheless, between half and two thirds of the successful females laid a second clutch. The low adult survival rate (Enemar & Nilsson 2008) together with an even lower, although unknown, survival rate of the juvenile birds may strongly select for double-broodedness. Therefore, the best strategy to maximise the presence of own reproducing offspring in the next generation is probably to be double-brooded.

The single-brooded female

A good strategy could also be to remain single-brooded, as at least third of the females that had fledged their first brood did not breed a second time. A large number of investigations regarding other double-brooded small passerines (references below) indicate that the frequency of single-brooded pairs may depend on 1. the weather conditions around the fledging time of the first brood, 2. the size of the first clutch and its eggs, 3. the timing of the start of breeding, 4. the quality of the female and of the territory, and 5. the age of the female. The relation between the listed factors and breeding behaviour has not been experimentally investigated in the study area. However, the descriptive information in the Results section makes it possible to assess the relevance of the listed factors.

1. Periods of rainy and cold weather or scarcity of food may inhibit a second breeding attempt. The breeding Treecreeper is very sensitive to bad weather, which often leads to desertion of nests containing eggs or young (Enemar 1995) (see also year 1996 in Table 1), thus indicating that an environmental impact on the frequency of laid second clutches is plausible.
2. Single and double-brooded females laid first clutches of the same size and comprising eggs of the same volume (see Results). This indicates that the Treecreeper has not evolved the trading-off strategy between single-broodedness with larger clutches and double-broodedness with smaller clutches, as experimentally demonstrated by e.g. Lindén (1988) in the Great Tit and Siefferman & Hill (2008) in the Eastern Bluebird *Sialia sialis*. The equal clutch size of the two categories of females is a trait not unique to the Treecreeper, as it also applies to e.g. the Song Sparrow *Melospiza melodia* (Smith & Roff 1980) and the Snow Bunting *Plectrophenax nivalis* (Smith & Marquiss 1995).
3. In contrast to some other double-brooded passerines (e.g. Banbura & Zielinski 1998, Weggler 2006, but see Evans Ogden & Stutchbury 1996) the single-brooded Treecreepers did not start laying later than the double-brooded pairs. Thus the Treecreepers do not postpone the laying, which would lead to increased clutch size due to the course of the “calendar curve” as described by e.g. Lack (1954) and Crick et al. (1993). Nor did the single-brooded Treecreepers fledge their broods later in the season than the double-brooded pairs. This indicates that the species does not comply with the “date hypothesis”, which was experimentally tested and demonstrated in the Great Tit by Verboven & Verhulst (1996).
4. Possible differences in individual and territorial quality between the single and double-brooded pairs, as discussed by Drent & Daan (1980), have not been investigated in this study. The fact that the clutch size and egg volume of the two breeding strategies did not differ (point 2 above) indicates that the females in question may be of equal quality (but see Smith et al. 1995). However, the quality of their territories is unknown.
5. The effect of age on the frequency of repeat broods can be preliminarily evaluated by using the information from the five seasons 1997 to 2001 (Table 1). Most probably the majority of the females that start breeding unringed are first-year breeders (Enemar & Nilsson 2008). In any case, they are, on average, one year younger than the returning females that have been ringed the previous season. No less than 15 out of 22 unringed birds (68%) laid second clutches in comparison to a mere 5 out of 13 ringed birds (38%). Although the difference is not statistically significant (Gadj=2.959, $0.10>p>0.05$), perhaps due to the small sample size, it does not rule out the possibility that the frequency of second clutches declines with age. If so, it is contrary to what has been found in other passerine species (e.g. Hario 1997, Banbura & Zielinski 1998, Weggler 2006) but it may be supported by the fact that the egg size decreases from the first to the second breeding season in the Treecreeper as a suggested consequence of senescence (Enemar & Nilsson 2008).

To conclude, the first of the five factors listed above seems to have the greatest influence on the frequency of single-brooded Treecreeper females, i.e. the prevailing environmental conditions around the fledging time of the first brood. The females could be expected to refrain from a second laying when the prospects of success seem so poor that the average addition to the reproductive result tends to be less than the advantage of using the late season to improve physical condition and increase the winter survival rate. Therefore they appear, on average, as more productive and fitter than the double-brooded females in cases where the second breedings of the latter fail. Moreover, the co-operation between the single-brooded parents is probably a more efficient method of raising high quality fledglings than that of the double-brooded pairs, where the feeding around the fledging day is to a varying extent left to the male alone, while the female is away preparing for the second breeding (own observations). Consequently, both breeding strategies are conserved in the gene pool of the population and found side by side during most seasons in the study area.

The replacement-breeding female

A Treecreeper female that has lost her first nest containing eggs or young has to decide whether to make a new breeding attempt or give up and instead improve her physical condition in order to survive the winter and breed again. The latter option is risky, because the adult survival rate is low, only about 32% (Enemar & Nilsson 2008, but see Peach et al. 1995). As plenty of breeding time remains after the breeding failure, as demonstrated by the double-brooded females, most or all of the failed females attempt to rear a replacement brood (see Results). The laying capacity can be considerable, as demonstrated by one female that finally succeeded in fledging the last of three consecutively laid 6-egg clutches. Apparently, the failed female has no better alternative but to invest in replacement breeding attempts while there is still time, despite the fact that it only implies "making the best of a bad lot" as described below.

To what extent, then, does the replacement breeding compensate for the failed first attempt? The size of replacement clutches did not differ from that of successful ones, i.e. clutches of the single-brooded female and the first clutch of the double-brooded female (see Results). However, the eggs of the replacement clutches were significantly larger and heavier than those of the first and second clutches, even after controlling for the effect of clutch size and temperature (Table 4). This means that the replacement-breeding females produce the heaviest hatchlings, especially as the Treecreeper hatchling increases in weight proportionally more than the weight increase of the egg, a unique situation among investigated small passerines (Enemar 2001). It is possible that the heavier hatchlings have a better start than those of the first brood, with increased prospects of reaching reproductive age, although studies supporting a positive relationship between egg size and offspring fitness among passerines are equivocal (Williams 1994, Christians 2002, but see Wagner & Williams 2007).

A number of the replacement-breeding females will continue to fail due to depredation, bad weather and other untoward events, resulting in a zero result for the season's breeding attempts. The presumptive single-brooded females that re-breed after failing may fully compensate for the interrupted first brood, even if negative consequences, i.e. the cost of the wasted investment in the first brood and the delayed breeding start, are unavoidable compared with the successful single-brooded females. Both aspects may negatively affect the restoration of their physical condition for the winter period ahead. The larger eggs and heavier hatchlings of the replacement clutch may compensate for only a tiny share, if any, of this loss of fitness. As mentioned above, the presumptive double-brooded and re-breeding female is prevented by lack of time from rearing a second replacement brood. Therefore the failed first brood means a heavier reproductive loss for this category of breeding Treecreepers. Obviously, the presumptive single-brooded and double-brooded females behave in the same way after failure and cannot be identified when acting as replacement breeders. The unavoidable reproductive shortcomings of the replacement-breeding Treecreepers compared to the successful single-brooded as well as double-brooded pairs indicate that those Treecreepers that start breeding early in spring and minimize the risk of failure by choosing good territories and safest possible nest sites are strongly favoured by natural selection.

The contribution of the three breeding categories to the total output of fledged broods

The calculations below are a simplified application of the precise and exhaustive method employed by Bryant (1979) to investigate the "reproductive values of the breeding patterns" in a House Martin *Delichon urbica* population. They were carried out in order to allow certain comparisons, in the area of "reproductive pattern", between my population and the investigated Treecreeper populations in Finland and Lithuania. The fledged brood was used as a unit when measuring the reproductive output, because the number of fledglings in each brood is often unknown.

The "reproductive quotient" was calculated, i.e. the quotient between the total number of fledged broods in the population and the number of breeding pairs. The percentage distribution of the fledged broods among the three breeding categories was also calculated. The totals of the breeding parameters in Table 1 have been used, both the original ones as well as those adjusted to approximately compensate for overlooked repeat broods. The resulting values are averages of the seasons and provide a rough idea of the "reproductive efficiency and pattern" of the study area population. The calculations are based on the rate of failed first breeding attempts and the proportion of the replacement breeding attempts together with the frequencies of fledged broods of the double and single-brooded pairs. The calculations were carried out on the assumption that the failure rate holds not only for the first broods but also for the second and replacement broods. The results are presented in Table 5 with the values based on the adjusted data in parentheses.

The reproductive quotient of the population of

Table 5. Frequency of failed and repeat broods, reproductive quotient (number of fledged broods per breeding pair) and percentage distribution of the total number of fledged broods among the three breeding categories as established in three different study areas. Numbers in parentheses denote adjusted values (see text).
Frekvensvärden för boförluster, andrakullar och omläggningar, samt förökningskvoten (antalet flygga kullar per häckande par) och den procentuella fördelningen av totalantalet flygga kullar på de tre häckningskategorierna i tre olika provytor. Siffrorna inom parentes gäller uppräknade värden (jfr huvudtexten).

	Proportion of (%) *Andel (%)*			Reproductive	Breeding category (%) *Häckningskategori (%)*		
Locality, nest site *Plats, bolägen*	Failed broods *Boförluster*	Second broods *Andrakullar*	Replacement broods *Omläggningar*	quotient *Förökningskvot*	Double-brooded *Tvåkullarpar*	Single-brooded *Enkullpar*	Replacement-breeding *Omläggarpar*
This study, nest pockets *Denna studie, häckningsfickor*	50 (50)	51 (66)	71 (100)	0.80 (0.92)	47 (54)	31 (19)	22 (27)
SW Finland, nest boxes *holkar*	29.8*	6.9*	0.89*	46	52	2	
Lithuania, natural *Litauen, naturliga*	45.4*	32.3*	22.1*	0.70	39	53	8

*) From Kuitunen & Aleknonis (1992).

the study area, representing a measure of the reproductive efficiency, is less than unity (0.80–0.92, Table 5) and implies that the total number of fledged broods is 10% to 20% less than the number of breeding pairs. Roughly speaking, the double-brooded pairs rear 50% of fledged broods in the study area, and each of the single-brooded and replacement-breeding pairs rear 25% of the remainder (Table 5). Had the population consisted of only single-brooded pairs, the quotient would have dropped to 0.75. Double-brooded pairs are the most efficient contributors in terms of fledged broods. This is true of most failure rates in the population and frequencies in the different breeding categories. Moreover, thanks to the double-brooded pairs, the quotient will exceed unity when the brood failure rate is reduced to about 40% or less (the other parameters remaining unchanged), i.e. a reproductive efficiency that is impossible to attain in an exclusively single-brooded population. Obviously, the double-brooded pairs play an important role in maintaining the high reproductive rate that is necessary considering the low survival rate of the Treecreeper (Enemar & Nilsson 2008). Another adaptive consequence of the low survival rate is probably that so many, if not all, females start replacement breeding after a failed first attempt.

The frequency values used in the calculations above tend to differ from those obtained in a Finnish population breeding in nest-boxes and a Lithuanian population using natural nest sites (Kuitunen & Aleknonis 1992), both of which studies were conducted over many years. The Finnish study area is mainly covered by coniferous and the Lithuanian by mixed coniferous and broad-leaved forests. The breeding data that are used for the calculations are presented in Table 5.

The differences between the three investigations are considerable not only in terms of the habitat of the study areas but also their size, density of the Treecreeper populations, the number and density of breeding facilities, various environmental factors and the main aim and direction of the research programs. Close comparative interpretations are therefore not advisable, all the more so as they cannot be tested statistically. Nevertheless, a couple of observations deserve attention.

The Lithuanian investigation is of special interest because it is based on naturally breeding Treecreepers. The high rate of unsuccessful broods, about 45%, indicates that the frequency of failed breeding in my population, 50%, is not much higher than what may occur in a population breeding without access to a surplus of breeding facilities. According to Kuitunen & Aleknonis (1992), the disturbing trapping and ringing activities lead to a "surplus" of failed broods that could be substantial, at least 9% of all interrupted breeding attempts.

The three investigated populations differ significantly with regard to the frequency of the three breeding categories, with the replacement-breeding pairs as the most obvious example. The latter are very few in the Finnish and Lithuanian populations. This also applies to their percentage share of the reproductive output (Table 5). Regarding the Finnish and Swedish studies, the considerable difference in the density of nesting facilities (2.5 nest-boxes/km^2 and 80 nest pockets/km^2, respectively) might partly explain the dissimilar repeat nest frequencies. The high density of nest pockets may have made it easier to keep up with the re-laying activities in my study area.

The reproductive quotients and the distribution of the fledged broods among the three breeding categories (both my calculations) are presented in Table 5. The frequency of the single-brooded pairs and their contribution to the total offspring production in Finland and Lithuania considerably outnumber the corresponding data for my population. This is a consequence of the fact that only about 33% of the successful first broods are followed by second breeding attempts, i.e. only about two thirds or less of the percentage found in my study area, as stated above. Obviously, the low frequency of established repeat broods (second and replacement broods) is the main cause of these differences. Compared with the Swedish population, the low rate of repeat broods in the Finnish population is compensated for by a lower failure rate, which means that a larger part of the population, the single and double-brooded pairs, produces at least one fledged brood per pair. Moreover, the second broods of the relatively fewer double-brooded pairs in Finland have a higher fledging rate due to the lower failure frequency. To conclude, the average number of fledged broods per breeding pair, the reproductive quotient, is about the same in the three populations (Table 5), with the naturally breeding Lithuanian population tending to lag slightly behind.

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Sammanfattning

Trädkryparen är en liten stannfågel som börjar att häcka tidigt på våren. Enligt forskare med erfarenhet från andra arter, kan en fågel med de nämnda egenskaperna förväntas föda upp två kullar årligen och dessutom uppvisa en bågformad kullstorlekskurva (den s.k. kalenderkurvan) under den långa häckningssäsongen. Kurvan visar att äggkullarna är relativt små i början av säsongen för att sedan successivt öka fram till säsongmitten, varefter de minskar igen. Allt detta stämmer in på trädkryparen, vilket tidigare visats och även kan utläsas av Tabell 3. Syftet med denna uppsats är att identifiera och närmare skärskåda trädkryparens tre kategorier av häckande par. Dessa är 1. par eller honor, som föder upp endast den först värpta kullen, här benämnda ”enkullpar” eller ”enkullhonor”, 2. ”tvåkullarpar” eller ”tvåkullarhonor”, som satsar på att få två kullar flygga, nämligen en förstakull och en andrakull, samt 3. ”omläggarpar” eller ”omläggarhonor”, vars häckningssätt uppkommer av tvång som följd av att första häckningen misslyckats på grund av

borövning, hårt väderläge eller annan störning, varefter ett eller flera nya försök görs för att få en omläggningskull flygg. Den mängd häckningsdata, som insamlats under en 10-årsperiod, redovisas i sammanfattad form i syfte att karakterisera delar av de olika häckningsförloppen i populationen. Därtill undersöks dels hur effektiv provytans population är på att producera flygga kullar, dels hur stora de olika häckningskategoriernas andelar är i denna produktion. Bland fältarbetets brister bör främst nämnas att antalet flygga ungar ej kunnat bestämmas under senaste delen av säsongen samt att variationen i näringstillgången ej studerats.

Metoder

Studierna genomfördes 1995–2005 (med uppehåll 2004) i Gunnebo-området, ca 10 km sydöst om Göteborg, i en 2,5 km^2 stor provyta. Denna är till största delen täckt av ädellövskog med inslag av planterad granskog. De öppna ytorna består mest av betad ängsmark. Provytan är försedd med 200 häckningsfickor, gjorda av takpapp och särskilt anpassade för trädkrypare (se Enemar 1992). Varje häckningsficka innehållande bo med ägg täcktes av perforerad aluminiumplåt som skydd mot angrepp av större hackspett. Den häckande trädkryparhonan fångades genom att fösas ut ur häckningsfickan rakt in i en genomskinlig plastpåse. Hon försågs därefter dels med en metallring, dels med en för varje individ unik kombination av tre färgringar. Ringmärkningen genomfördes för att eventuell förekomst av andrakullar och omläggningskullar skulle kunna påvisas senare under säsongen. Häckningsfickorna inspekterades med varierande tidsmellanrum beroende på forskningsuppgiftens karaktär för säsongen, dock alltid tillräckligt ofta för att säkert kunna räkna antalet häckningar och följa dessas förlopp. För varje tvåkullarpar och omläggarpar mättes avståndet mellan de använda häckningsfickorna på en kartskiss i skala 1:10000. Temperaturdata hämtades från mätningarna vid Säve flygplats (SMHI 1995–2005) vilka tidigare visats stämma väl med temperaturen i provytan. Volymen eller storleken på äggen beräknades med hjälp av måtten på längden och bredden. Äggmätningarna gjordes på fotografier av genomlysta kullar (se Enemar 1997, 1999).

Resultat med kommentarer

De häckande trädkryparnas fördelning på tvåkullarpar och omläggarpar presenteras i Tabell 1. Även antalet enkullpar redovisas där (se spalten ”None”) liksom de tidiga förstakullarnas fördelning på fullföljda och avbrutna häckningar. I genomsnitt fick hälften av paren sin förstakull flygg. Av dessa par startade runt 50% därefter en andra kull (tvåkullarparen), medan resten (enkullparen) avstod från en ny satsning. Av de par som misslyckats, gjorde ca 70% ett nytt häckningsförsök (omläggarparen). Andelen såväl tvåkullarpar som omläggarpar är hög jämfört med erfarenheterna från finska studier (ca 30% resp. ca 10%). Icke desto mindre kunde antalet upprepade häckningar i provytan misstänkas vara för lågt. Anledningen är att beräkningarna bygger på förutsättningen, att alla trädkrypare vid förnyade häckningsförsök stannar inom provytan och därtill väljer en häckningsficka som ny boplats. Används naturliga boplatser kommer dessa att förbises och antalet enkullpar därmed att överskattas och antalet tvåkullarpar och omläggarpar att underskattas. Följande fakta talar dock för att de allra flesta häckande paren höll sig till fickorna vid upprepade häckningsförsök: 1. De trädkrypare som återkommit efter övervintringen har häckat nära eller ibland i fjolårets häckningsficka. 2. Förflyttningarna mellan två häckningsförsök samma säsong var mycket korta (se nedan). 3. Tillgången på lediga häckningsfickor har varit riklig (medeltätheten häckande har varit 5 par/km^2 med 80 fickor/km^2 till förfogande). 4. Inte ett enda trädkryparbo har upptäckts utanför fickorna inom provytan i samband med fältarbetet. Men mot dessa fyra punkter talar det faktum att i medeltal tre icke ringmärkta honor dykt upp sent och häckat i provytan i juni varje år. Det är rimligt att anta, att denna inflyttning till provytan har motsvarats av ungefär lika stor utflyttning av områdets färgmärkta honor i syfte att starta säsongens andra och därmed förbisedda häckningsförsök. Tas hänsyn till detta, blir andelen andrakullar och omläggningar något högre jämfört med värdena i Tabell 1. Resultatet av denna uppräkning blir att mellan hälften och två tredjedelar av de flygga förstakullarnas honor värper en andrakull medan resten avstår. Vidare gör i stort sett alla honor med avbrutna förstakullar ett nytt häckningsförsök.

Häckningssäsongens tidsschema framgår i grova drag av Tabell 2, som visar tidsåtgången för de olika momenten i häckningen för tvåkullarhonan och omläggarhonan. Skillnaden mellan dem vad gäller säsongens längd, räknad från första kullens första ägg till sista kullens utflygning, var i medeltal endast ca en vecka, en liten men statistiskt säker skillnad. Man hade annars väntat sig mer eftersom omläggarhonans första häckning ofta avbröts åtskilliga dagar (medelvärde 17 dagar) innan kullen skulle ha flugit ut. Hon hade därmed haft möjlighet att börja omläggningen långt innan tvåkullarhonan kunde börja värpa sin andrakull. Av någon anledning har det gått trögt för omläggarhonan att få igång den nya häckningen. Tvåkullarhonan har däremot förberett sin andra häckning (bobygge, äggutveckling m.m.) i så god tid att första ägget ibland värpts redan dagen efter första kullens utflygning. Detta var möjligt tack vare att hanen matade ungarna oftare än honan, stundtals ensam, under dagarna strax före och efter utflygningen. Hanen tog sedan skadan igen genom att så gott som helt utebli från matningen av den något mindre andrakullen, som honan trots sin ensamhet ofta nog lyckades få på vingarna.

Den ”trögstartade” omläggarhonan värpte den nya kullens första ägg i medeltal först 9,5 dagar efter katastrofen med första kullen (Tabell 2). Jämfört med den lyckosamma honans andra kull tog det dessutom två dagar längre tid att få omläggningsungarna flygga. Dessa förseningar bidrog uppenbarligen till att den resterande säsongen blev för kort för att räcka till uppfödning av ytterligare en kull, eftersom inga försök till en andra kull har kunnat noteras efter de många kontrollerade omläggningskullarnas utflygning.

Medeldatum för första kullens start och ungarnas utflygning var densamma för alla kategorier av häckande par.

Medelavståndet mellan häckningarna var för 32 tvåkullarpar 146±90 m och för 40 omläggarpar 166±110 m. Medelskillnaden på 20 m är inte statistiskt säker. Man hade annars väntat sig att de honor som misslyckats, t.ex. genom att boet rövats, skulle flytta längre bort än de som lyckats med första kullen. I stället valde en tredjedel av båda kategorierna den närmaste häckningsfickan i grannskapet för den nya kullen och en tiondel en ficka mer än 250 bort.

I Tabell 3 redovisas antalet ägg i de tre olika häckningskategoriernas kullar för varje tio- eller elvadagarsperiod under säsongen. Summaraden längst ned i tabellen avspeglar den bågformade kullstorlekskurvan under säsongen med sin topp i mitten, dvs andra perioden i maj. Det är som synes omläggarhonorna som då svarar för äggläggningen. Sorterar man fram de förstakullar, som svarar mot de 36 andrakullarna i tabellen, visar det sig att medelantalet ägg i förstakullen (5,51±0,56) är signifikant större än i den påföljande andrakullen (5,22±0,72). Motsvarande jämförelse för omläggningskullarna visar att ingen skillnad föreligger mellan den havererade förstakullen och omläggningskullen.

Även det enskilda äggets medelvolym kan variera mellan de olika kategorierna av kullar, vilket framgår av Tabell 4. Tvåkullarhonan värper lika stora ägg i båda kullarna. Men räknar man bort ”den hjälp” honan fått av varmare väder och lägre äggantal under andra kullens värpperiod, så hade äggen blivit signifikant mindre. För omläggarhonan är det tvärtom. Honan värper klart större ägg i andra häckningsförsöket, vilket betyder att de nykläckta ungarna också blir är större. Det råder nämligen ett klart positivt samband mellan äggets och den nykläcktas storlek hos trädkryparen (se Enemar 2001). Om sedan en nykläckt unge på sikt har någon fördel av att vara särskilt stor är fortfarande en omtvistad fråga. Enkullhonans ägg är lika stora som tvåkullarhonans och omläggarhonans ägg i förstakullen.

Diskussion

Att värpa en kull till eller ej, det är frågan

Eftersom trädkryparen är en etablerad uppfödare av två kullar, kan den i rubriken ställda frågan verka onödig, i synnerhet som det visats för andra arter att de honor, som försöker sig på att dra upp två kullar genomsnittligt får fler ungar på vingarna än de som nöjer sig med en enda flygg kull. Man kan därför förvänta sig, att alla trädkryparpar har siktet inställt på att föda upp två kullar. Men däri ligger ett moment av chansning. Detta skall här något kommenteras tillsammans med synpunkter på de övriga häckningskategoriernas för- och nackdelar.

De honor, som lyckats få säsongens först värpta kull flygg, har gott om tid att häcka en gång till. Vinsten är alltså uppenbar, men det finns även skäl att ”tänka sig för”. En andrakull innebär nämligen en mödosam arbetsinsats som tär på en honas krafter utöver vad den lyckade förstakullen redan kostat och detta i synnerhet som trädkryparhanen endast obetydligt eller inte alls deltar i matningen av andrakullen. Den konditionskrävande dubbla häckningen innebär för honan, att hon kommer i ett sämre läge vad gäller att bygga upp nödvändig styrka för att framgångsrikt klara instundande övervintring. Icke desto mindre väljer bortåt två tredjedelar av de framgångsrika honorna i provytan att satsa på en andrakull. Detta torde vara taktiskt välbetänkt eftersom syftet med all fortplantning är att få egen könsmogen avkomma med i nästa generation, dvs i det häckande beståndet nästa säsong. Det angelägna i tvåkullartaktiken understryks av att trädkryparen är en mycket kortlivad art bland småfåglarna (endast 32% överlevnad enligt preliminära beräkningar på provytans bestånd), dvs chansen att klara sig över vintern och kunna häcka igen är under alla förhållanden ganska liten. Därtill kommer att den flygga avkommans överlevnad säkerligen är betydligt lägre. Därför torde den produktiva tvåkullartaktiken inom provytan under nuvarande förhållanden favoriseras av det naturliga urvalet.

Det kan dock inte vara ”helt fel” av en trädkryparhona att nöja sig med den utflugna första kullen för säsongen, eftersom runt en tredjedel av dem förblir enkullhonor. Många ornitologer har forskat i möjliga orsaker till detta val men med olika resultat, delvis beroende på vilken art som studerats. Det har föreslagits att väderförsämring och födoknapphet vid tiden för första kullens utflygning kan få en hona att avstå från en andra häckning. Sannolikt gäller detta för trädkryparen, eftersom arten påfallande ofta reagerar på dåligt väder genom att överge både ägg och ungar. Hos vissa arter värper honan antingen en stor kull (enkullhonan) eller två små (tvåkullarhonan), men ett sådant laborerande med kullstorlekar gäller ej för trädkryparen, eftersom förstakullarnas medelstorlek är densamma för en- och tvåkullarhonorna. Det kan tilläggas att någon skillnad i äggstorlek mellan dem inte heller föreligger. Denna likhet vad gäller ägg och kullar betyder sannolikt att de två honorna befinner sig konditionsmässigt på samma nivå. För andra arter har visats att enkullhonorna ligger efter i vikt, men detta gäller sannolikt inte för trädkryparen. Inte heller uppvisar de blivande enkullhonorna någon försening i häckningsstarten på våren jämfört med tvåkullarhonorna. Sammanfattningsvis verkar det sannolikt att det i många, kanske de flesta, fall är omständigheternas tryck (uselt väder, dålig näringstillgång) som hejdar en hona från att fullfölja sin häckningsdrift och värpa en andrakull.

Man kan fråga sig om vissa trädkryparhonor kan vara helt inställda på att producera en enda flygg kull för säsongen, alltså även under gynnsamma omständigheter. I så fall borde denna häckningsmodell, i varje fall i vissa lägen, medföra någon eller några fördelar jämfört med tvåkullarhonans häckning. En sådan kan vara att enkullhonan kan ägna all sin tid att delta i matningen av kullens ungar tillsammans med hanen ända fram till självständighet. Resultatet av samarbetet bör bli en avkomma av bättre kvalitet och högre överlevnad jämfört med tvåkullarhonans förstakull, som mot botidens slut och därefter mer eller mindre lämnas därhän av honan, som blivit upptagen med att förbereda andrakullen (bobygge, äggbildning, m.m.). Enkullhonan får däremot gott om tid att rugga och bygga upp sin kondition inför vintern med förhöjd överlevnadschans som följd. Dessa fördelar blir än mer uppenbara i jämförelse med de många tvåkullarhonor som misslyckas med andra häckningen, alltså en konditionskrävande satsning utan resultat med risk för sänkt vinteröverlevnad. I detta läge framstår enkullhonorna avgjort som vinnare i ”kampen” om det naturliga urvalets gunst. Både enkull- och tvåkullartaktiken kan alltså ha sina fördelar och därmed chans att tillämpas samtidigt i ett och samma trädkryparbestånd.

Den trädkryparhona som misslyckats helt med första kullen står inför valet att antingen starta en ny häckning eller också ägna resten av säsongen till att rugga och bygga upp sin kondition inför vintern och sikta på nästa säsongs häckning. Detta senare är en riskfull chansning eftersom trädkryparen, som ovan påpekats, är så kortlivad. Icke oväntat värper därför så gott som alla honor på nytt en kull, som är lika stor som den första. De har därmed ersatt den förlorade kullen fullt ut oberoende av om förlusten drabbat en blivande enkullhona eller tvåkullarhona. Däremot finns ej tid att efter en lyckad omläggning föda upp ytterligare en kull och uppnå den från början avsedda produktionsnivån som tvåkullarhona. Den hona, som fått en omläggningskull flygg, befinner sig förmodligen i visst underläge även gentemot den framgångsrika enkullhonan, eftersom den förspillda kraftinsatsen på den misslyckade första häckningen tillsammans med den senarelagda enda flygga kullen kan betyda att hon inte hinner nå toppkondition innan vintern sätter in. En omläggarhona får finna sig i att med sin nya kull förhoppningsvis i alla fall undvika att drabbas av vad värre är, nämligen en häckningssäsong helt utan avkomma.

Sammanfattningsvis tycks följande gälla för provytans population: Den trädkrypare är framgångsrikast som börjar häcka tidigt på våren med säker boplacering i ett näringsrikt revir och som hinner med att föda upp två kullar. Den förlust som ett avbrutet första häckningsförsök innebär kan aldrig fullt ut repareras genom omhäckning.

De olika häckningskategoriernas andel i populationens totala produktion av flygga kullar

Dessa beräkningar utfördes för att möjliggöra jämförelser med andra trädkryparpopulationer, gällande främst sammansättningen av de olika häckningskategorierna och produktionen av flygga ungar. Eftersom antalet flygga ungar inte är känt för alla häckningar, används istället antalet flygga kullar vid jämförelsen. Resultaten är sammanfattade i Tabell 5.

Den i tabellen angivna ”förökningskvoten” för provytans trädkryparbestånd erhålls genom att totala antalet flygga kullar divideras med totala antalet häckande par. Som synes är kvoten mindre än ett (Tabell 5), vilket betyder att flera par misslyckats helt med att få en kull flygg. Detta beror på att andelen boförluster varit så omfattande, 50% (Tabell 1). Att kvoten ändå är så hög, beror på att tillräckligt många tvåkullarhonor lyckats med båda häckningarna men även på att de olycksdrabbade honorna efter den avbrutna första häckningen i så hög grad startat ett nytt häckningsförsök (Tabell 1). Som väntat är fördelningen av flygga kullar på de tre häckningskategorierna ojämn. Tvåkullarparen svarar för omkring hälften av antalet flygga kullar i provytan, medan enkullparen och omläggarparen vardera står för ungefär hälften av återstoden (Tabell 5).

Avslutningsvis görs en enkel jämförelse med resultaten från en finsk undersökning som bygger på häckningar i trädkryparanpassade holkar i barrskog, och en litauisk, där naturliga boplatser letats upp i blandskog. Studiernas olikartade karaktär tillåter inte att mer ingående jämförelser görs. Men man kan lägga märke till att förökningskvoterna är mindre än ett i båda fallen och av samma storleksordning som den i provytan (Tabell 5). Boförlusterna är betydande och ligger omkring 30% i den finska och 45% i den litauiska studien, varav de finska tenderar att vara färre än i provytan. Frekvensen omläggningar är klart lägre, 7% resp 22%, vilket avspeglas även i den låga andelen omläggningskullar i den totala produktionen av flygga kullar (Tabell 5). Detta torde vara den enda säkra skillnaden jämfört med beståndet i provytan. Den är emellertid svårtolkad och kan möjligen till icke ringa del bero på att i den finska undersökningen vissa omhäckningar inte fångats upp av holkarna. Detta kan i sin tur vara en följd av att det tillgängliga antalet holkar i den finska populationen varit avsevärt lägre än antalet häckningsfickor i provytan (2,5 holkar/km^2 resp. 80 häckningsfickor/km^2). En tätare uppsättning av häckningsanordningar torde rimligen innebära en säkrare registrering av andrakullar och omläggningar.

Den låga andelen förnyande häckningar (andrakullar och omläggningar) i den finska och den litauiska studien tillsammans med de färre boförlusterna motsvaras av högre frekvens av framförallt enkullhäckningar. Dessa svarar för störst andel i produktionen av flygga kullar. Även tvåkullarhäckningarna har ganska stor andel trots den klart lägre frekvensen par jämfört med beståndet i min provyta, vilket återigen är en effekt av den nyssnämnda låga nivån på boförlusterna.

Nya böcker – *New books*

John Ash and John Atkins, 2009: **Birds of Ethiopia and Eritrea**. Christopher Helm, London (beställningar: www.acblack.com; £45,00).

Nigel Redman, Terry Stevenson och John Fanshawe, 2009: **Birds of the Horn of Africa**. Christopher Helm, London (beställningar: www.acblack.com; £29,99)

Dessa två böcker om fåglarna på Afrikas Horn kompletterar varandra väl. Den förstnämnda är en atlas över fåglarnas utbredning plus litet geografi, politik och utforskningshistoria. Den andra är en traditionell fälthandbok med fåglarna i färg och korta hjälptexter. De täcker något olika områden, atlasen enbart Etiopien och Eritrea medan handboken också tar med Djibouti och Somalia. Böckerna passar också bra för SOF/Avifauna som haft resor till Etiopien sedan 2006, och som aviserat en ny resa 2010.

Atlasboken täcker en sammanlagd yta av 1.258.000 kvadratkilometer, alltså tre gånger Sveriges landareal. Utbredningskartorna upptar 291 av de 463 sidorna och de har en upplösning på en halv gånger en halv grad. Det gör att fåglarnas förekomst redovisas i ungefär 460 rutor som var och en omfattar ungefär 3000 kvadratkilometer. Jämfört med många enskilda länders atlaser är upplösningen grov, men det är ändå otroligt imponerande att ha presterat en sådan atlas. Upplösningen är nämligen ungefär densamma som i EBCC:s atlas över Europas fåglar (rutstorlek 2500 kvadratkilometer). Och, häpnadsväckande, de två författarna har själva besökt 346 av rutorna. Övrig information kommer från andra rapportörer och från litteraturen. Totalt har man registrerat 872 fågelarter i de två länderna tillsammans, varav 527 häckar och minst 200 är plaäarktiska flyttfåglar. Regionen är sedan länge känd för endemer och hela 32 fågelarter, möjligen litet frikostigt räknat, finns ingen annan stans i världen.

Boken inleds med ett intressant kapitel om ornitologins historia. Som i de flesta delar av världen började den mera systematiska utforskningen i slutet av 1700-talet då museer och samlare från de ”civilicerade” länderna började sända expeditioner till jordens alla hörn, oftast kopplade till ekonomisk erövring eller inbördes konkurrens om herravälde. Från berättelsen om en sådan expedition må ett kort utdrag relateras. Det var kejsar Tewodros den andre som 1867 hade fängslat den brittiske konsuln och några andra européer. England kunde inte tolerera detta. Fångarna måste befrias och 33.000 man, 20.000 mulåsnor, 280 fartyg, flera elefanter och en järnväg rekryterades. Med bland folket fanns inte bara krigare utan också gott om forskare, bl.a. naturforskare. Så mycket naturforskning blev väl inte gjord, ty redan i april året efter var expeditionens uppgift slutförd, kejsaren hade tagit livet av sig och engelsmännen hade stulit kronjuvelerna och farit hem igen. Men det är till stor del utländska tjänstemän, läkare, specialister, militärer, missionärer, resenärer, etc. som står för den mesta informationen om fåglarnas förekomst.

Regionen har ständigt varit politiskt orolig och är det fortfarande. Detta i kombination med begränsade kommunikations- och boendemöjligheter i stora delar av området har gjort att det i dag inte förekommer något omfattande modernt fågelskådande, även om Avifauna och en del andra resebyråer börjat skåda i regionen. Topografiskt och klimatiskt finns nästan allt, från tropiska regnskogar till höga berg (4300 m), öknar och stora marina arkipelager. Väldigt mycket om fåglarnas förekomster är fortfarande dåligt känt och nästan varje resa i den nya vågen av fågelturism bidrar med nya kunskaper trots att det är mest inarbetade lokaler som besöks.

Efter kartdelen finns nyttig statistik: förteckning över de viktiga fågelområden som BirdLife International identifierat, rödlistade arter, arter med begränsad utbredning samt, och icke minst, en lista över tusen fågellokaler med namn, höjdläge och exakta koordinater. Det är bara att ladda GPSen och dra iväg!

Denna atlasbok väcker en viktig fråga. I dag torde nämligen en stor del av den nya informationen om fåglarna i länder utan talrika inhemska ornitologer insamlas av besökande utlänningar. Vad händer med deras observationer? På nätet hittar man talrika reserapporter från både enskilda personers privata resor och gruppresor av Avifaunas typ. Men de flesta ornitologer skriver nog aldrig någon rapport, och frågan är väl om ens de som faktiskt har publicerats på nätet kommer till så mycket annan användning än som tips för nya resenärer. Redan i Europa är det svårt att ta reda på hur man skall rapportera iakttagelser. Om detta skulle SOF:s sakkunniga inom fågelrapporteringen kunna sammanställa praktisk information om vart man vänder sig och hur man går till väga för att rapportera fynd från särskilt svagt kartlagda länder.

Den illustrerade fälthandboken får väl sin första test av svenska ornitologer på Avifaunas resa 2010. Eftersom den täcker även Djibouti och Somalia kommer även Socotra, som tillhör Jemen, med. Där är ju fågelturismen rätt välutvecklad. Upplägget av handboken är sådan att färgbilderna ligger på höger sida och text och små kartor på vänster sida av varje uppslag. Boken bygger helt på att man skall kunna identifiera arterna, all annan information är marginell. Eftersom boken utkom i maj 2009 är den inte prövad i praktiken ännu. En snabb bläddring ger dock ett synnerligen gott intryck; arter jag känner till ser ut som de ska. Fast på kritiska arter är det ofta små detaljer som avgör. Framtiden får utvisa om det går att använda bilderna för att skilja på gransångare och östlig lövsångare i vinterdräkt! Men nyckeln finns med i texten: gransångaren vippar neråt med stjärten, vilket ingen ras av lövsångare gör. Det hela verkar förtroendeingivande. Illustrationerna är utförda av John Gale och Brian Small. En synnerligen viktig och värdefull bok, och den första över huvud taget för nordöstra Afrika. Korsningen mellan olika faunaregioner plus alla flyttare norrifrån gör att den behandlar runt tusen arter. Och på Afrikas horn, särskilt i bergen, finns det faktiskt fortfarande viss möjlighet att upptäcka en för vetenskapen ny fågelart.

SÖREN SVENSSON

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Instructions to authors

Allmänt gäller att bidrag skall vara avfattade enligt den modell som finns i tidigare häften av tidskriften. Titeln skall vara kort, beskrivande och innehålla ord som kan användas vid indexering och informationssökning. Uppsatser, men ej andra bidrag, skall inledas med en Abstract på engelska om högst 175 ord. Texten bör uppdelas med underrubriker på högst två nivåer. Huvudindelningen bör lämpligen vara inledning, metoder/studieområde, resultat, diskussion, tack och litteratur. Texten får vara på svenska eller engelska och uppsatsen skall avslutas med en fyllig sammanfattning på det andra språket. Tabell- och figurtexter skall förses med översättning till det andra språket. Manuskriptet bör sändas som epostbilaga till soren.svensson@zooekol.lu.se. Texten bör vara i format MS-Word. Figurer och tabeller skall inte inarbetas i den löpande texten utan sändas som separata filer. En papperskopia skall också sändas, och den skall innehålla eventuella orginalfigurer som inte kan sändas elektroniskt. Om nödvändigt tar vi också emot kortare manuskript på enbart papper.

Andra bidrag än uppsatser bör ej överstiga 2 000 ord (eller motsvarande om det ingår tabeller och figurer). De skall inte ha någon inledande Abstract men däremot en kort sammanfattning på det andra språket.

Författarna erhåller korrektur som skall granskas omgående och återsändas. Författare erhåller en pdf-fil av sitt bidrag.

Referenser skall i texten anges med namn och årtal samt bokstäver (a, b etc) om det förekommer referenser till samma författare och år mer än en gång. För litteraturlistans utformning se nedan.

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