Population turnover in groups of wing-moulting waterbirds: the use of a natural marker in Great Crested Grebes

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Introduction

The majority of waterbird species (divers, grebes, flamingos, swans, geese, ducks, rails, cranes and auks) renew their flight feathers by a simultaneous wing-moult (Stresemann and Stresemann 1966). Shedding all flight feathers at the same time results in an extended period of impaired flight capabilities. Flightlessness makes birds vulnerable, and therefore a location which provides safety from predators and sufficient food is critical during the moult period. Special habitat requirements may be the reason that many waterfowl undertake migration (often in the opposite direction to that followed in autumn) before undergoing replacement of the plumage (Salomonsen 1968). At the moulting sites the birds often assemble in large concentrations (Vlug 1976; van der Wal and Zomerdijk 1979; Campbell and Milne 1983; Little and Furness 1985; Storer and Jehl 1985). Protection from predators (including man) can be provided by distance from shore (e.g. open water for diving and sea ducks) or by cover (e.g. reedbeds for surface feeding ducks and geese). The specific habitat requirements may mean that the birds leave as soon as the moult is completed, leading to a large turnover at moulting sites.

Recent studies on moulting waterbirds have often recorded the numbers present, but never attempted to quantify the total number of individuals using a site through the period of the moult. This may by far exceed the numbers present at any one time. It should, however, be possible to quantify the turnover by sufficient regular observations. Firstly, all waterbirds have the habit of regularly flapping the wings, a comfort movement. During wing-flapping the stage of wing-moult can easily be seen. Secondly, since flight feather growth rates are directly proportional to the full-grown wing lengths (Prevost 1983), wings-in-moult in fact represent a natural marker from which periodicity can be estimated.

This study sets out to examine the necessary methodology, using Great Crested Grebes *Podiceps cristatus*. For more than 20 years these have congregated in large numbers (up to a daily maximum of 40,000 individuals) in Lake IJsselmeer, The Netherlands. It is the largest known moulting concentration of Great Crested Grebes in Europe (Piersma, Vlug and Westhof 1986). During the early morning and late afternoon the grebes forage on the open water. During mid-day and mid-night they assemble in one or more rafts on the shallow water within 2 km from the shore.

Study area and field methods

Fieldwork was done along the south coast of the province of Friesland (52°50′N, 5°28′E; inset Figure 1), where there is a 4 km long and 0.5 km wide stretch of reeds (the Mokkebank). For the first two km offshore the water is shallow (less than 2 m deep) is used by the Great Crested Grebes to roost, and is part of a protected nature reserve without access for the public.

The observations were made directly from the shore or from an elevated hide in the water's edge, at distances of 50–1500 m from the grebes. A 15–60 x zoom telescope was used. A manual counter was employed to sum the numerical units discerned. Due to their foraging rhythm, the numbers of grebes on the roosting area peaked between 12 and 16 hrs M.E.T. (Piersma *et al.* 1986). The daily totals therefore refer to counts made during these afternoon periods.

Wing-flapping (Figure 2) takes 2–8 seconds and it is usually easy to see whether the grebe is in wing-moult or not. Based on studies of drowned grebes collected from gill-nets by local fishermen, three moult phases could be discerned (Figure 3). Birds in phase 1 have just shed their feathers with primaries less than one-third of final length. Phase 2 birds have flight feathers up to two-thirds of final length. In phase 3 moult cannot be discerned. These birds are either non-moulting individuals or have nearly completed flight feather growth. The moult phase of each grebe which was seen when wing-flapping was recorded. Given sufficient samples, recording errors will average out.

The frequency of wing-flapping bouts was measured by focussing on subgroups of grebes in a roosting raft. The number of grebes in focus (N) was counted and the number of bouts (F) was recorded within a period (T), which was timed by a stopwatch in minutes. The bout rate is expressed per hour, and was calculated by dividing the number of bouts by the number of "grebe-minutes": (F/(NxT) x 60).

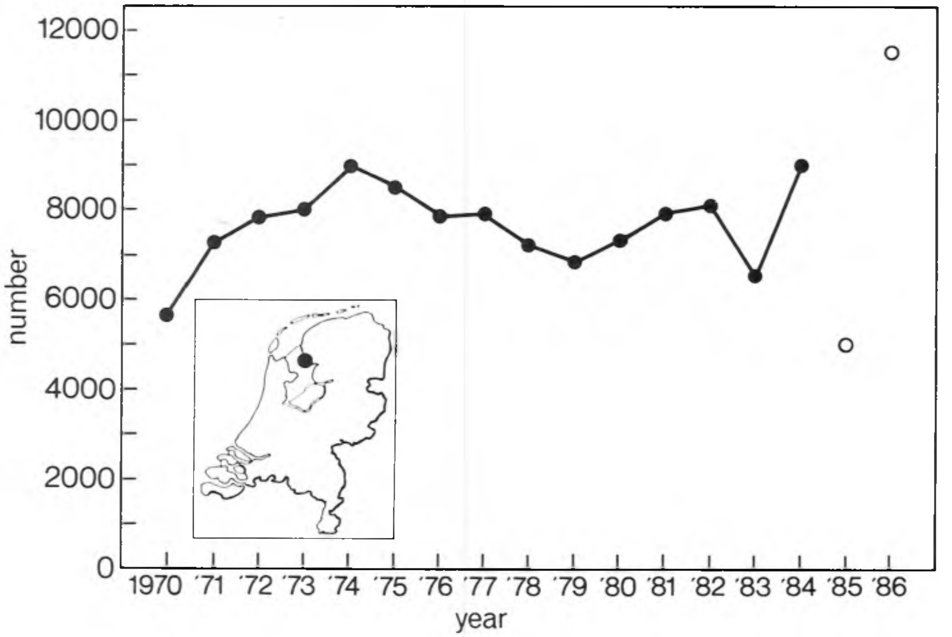

Figure 1. Average daytime numbers of Great Crested Grebes on the moulting area near the Mokkebank, Friesland (inset), in the period 1970–1986. Up to 1984 five-year running averages are given. The two open dots indicate the seasonal averages for 1985 and 1986.

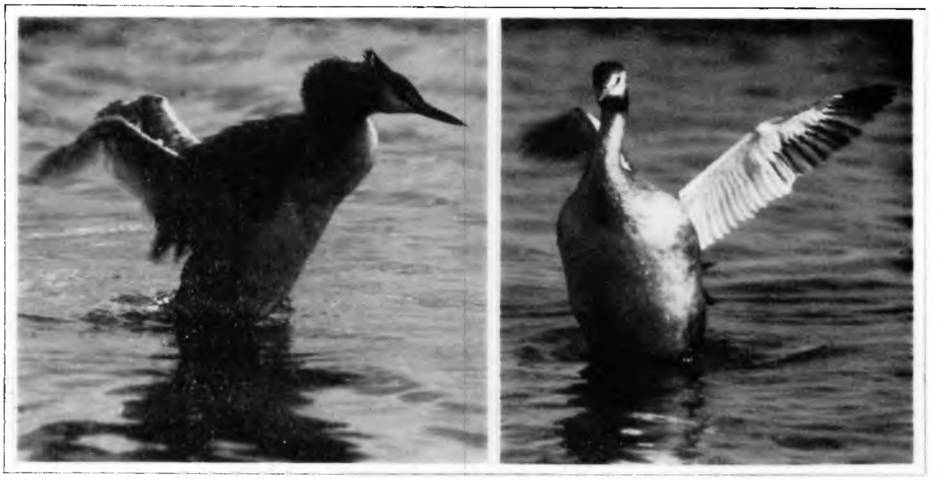

Figure 2. Two examples of wing-flapping Great Crested Grebes. The bird on the left has just shed the flight feathers (moult phase 1), whereas the bird on the right has almost completed wing-moult (moult phase 3). (Photo courtesy J. van de Kam.)

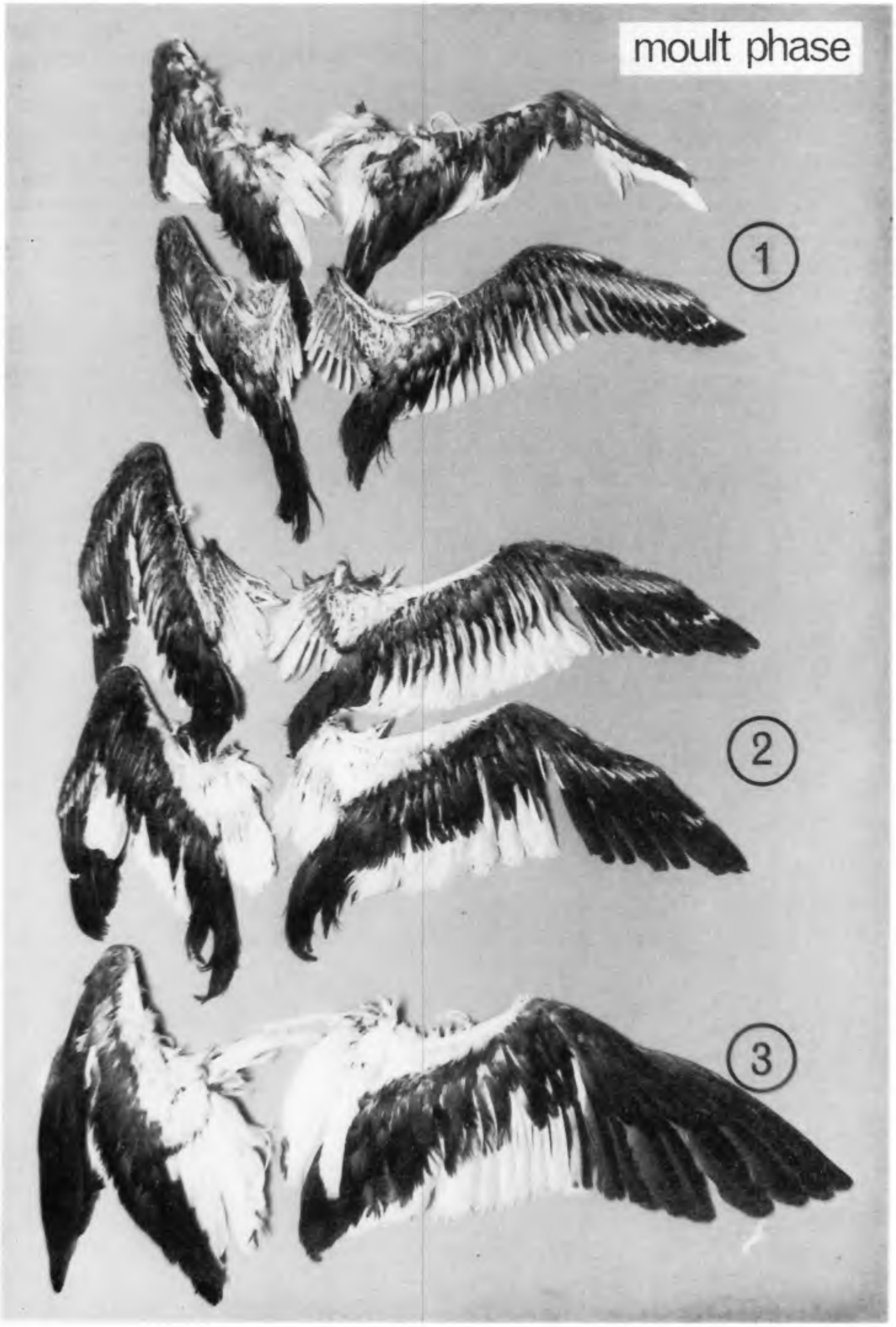

Figure 3. Illustration of the three different phases of wing-moult in Great Crested Grebes.

Results

The results of the observations in 1985 and 1986 on moult phase and total numbers of Great Crested Grebes on the day-time roost are presented in Figure 4. In both years the numbers present increased in early August. However, in 1985 there was a continuous decline from halfway through August onwards, and virtually no grebes roosted near the Mokkebank in the first week of September. Numbers then increased again. In 1986 no such temporary decline was apparent although the numbers fluctuated strongly. In 1985 and 1986 peak numbers were 8,000 and 18,000 respectively. The proportion of

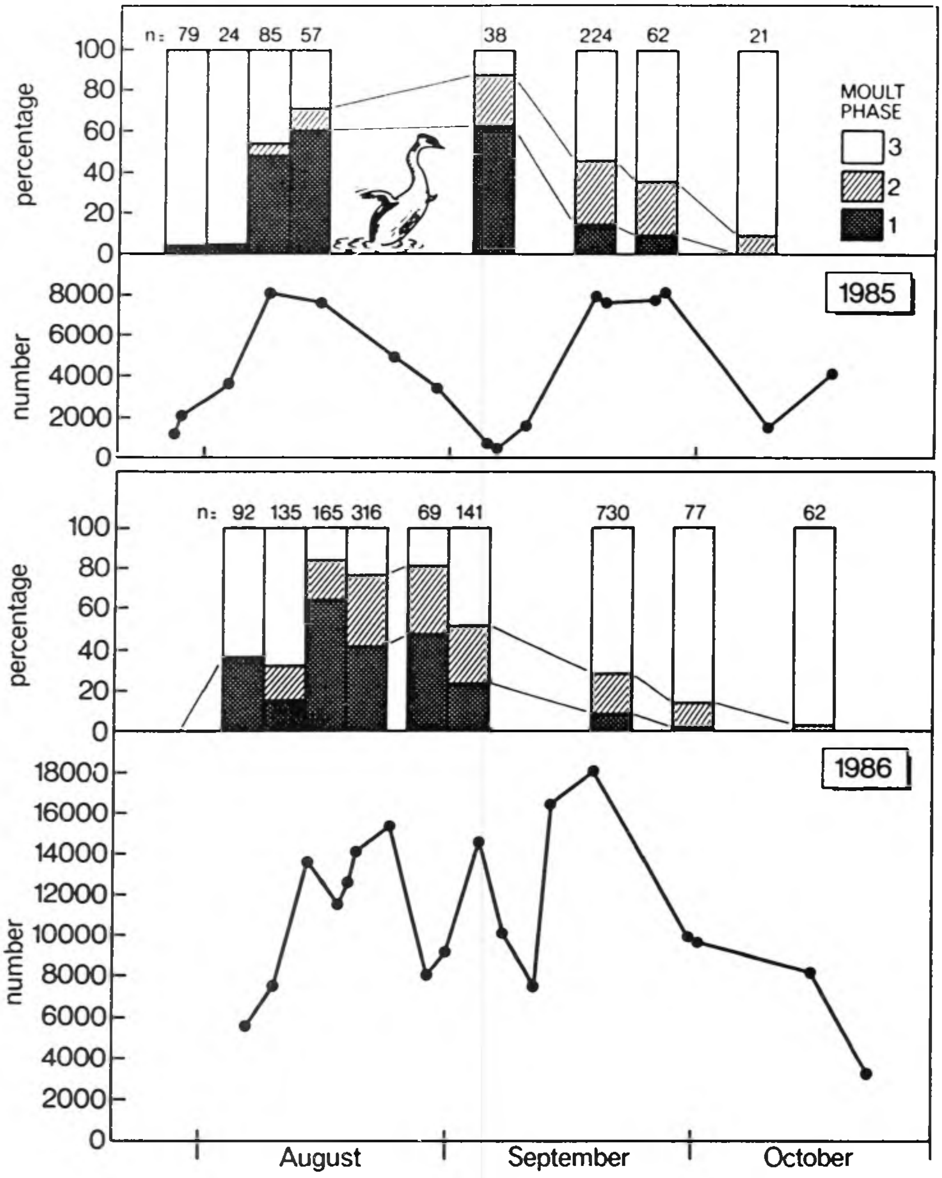

Figure 4. **Seasonal changes in the number, and moult phase composition, of Great Crested Grebes in 1985 (top) and 1986 (bottom).** n indicates the number of grebes per period that were examined for moult phase during wing-flapping. Data from the entire daylight period included.

grebes in moult phase 1 increased from about zero, to about 50% in the second week of August 1985, and peaked in early September. In 1986 wing-moult may have been somewhat earlier, with peak proportions of phase 1 halfway through August.

For a straightforward estimation of population turnover from total numbers present and moult phase composition, we need to know the duration of each moult phase (regarded as a marked "cohort"), and also, to ascertain whether the frequency of wing-flapping bouts is equal for moulting and non-moulting grebes. No direct measurements of wing-moult duration are available for Great Crested Grebes but a reasonable estimate can be obtained. Prevost (1983) showed that, between species, flight feather growth rate and wing length are linearly correlated, with only small differences between taxonomic groups. Highest feather growth rates in relation to final wing length were found in the simultaneously moulting Anseriformes. Great Crested Grebes, with an average wing length of 195 mm, would be predicted to have a growth rate of 6 mm/day (when using the linear relationship calculated from the Anseriform-data), or of 4 mm/day (when using the relationship based on data from all species). In one captive Black-necked Grebe *Podiceps nigricollis* (wing length 60% of that of Great Crested Grebes), Storer and Jehl (1985) found a growth rate of 3 mm/day. Since the average length of the primaries is 103 mm, a growth duration of 17–26 days is predicted (average 21 days). Because their protein-rich diet of fish probably imposes no growth limitations, the growth duration is likely to be closer to 17 than to 26 days. Independently, an average moult duration of 17 days was also estimated from a sample of 74 drowned grebes in active wing-moult, by regressing date on percentage of primaries' final length

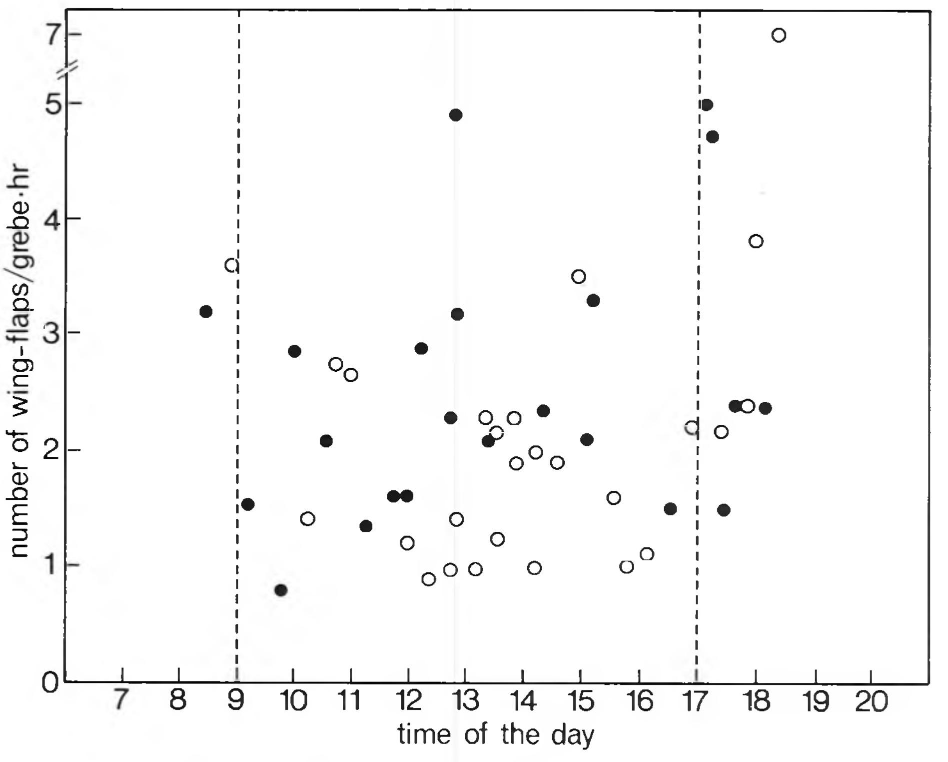

Figure 5. Daily variation in wing-flapping bouts of Great Crested Grebes. Filled dots indicate the measurements on 17th, 23rd and 28th August 1986 when daily average wing-flapping bouts varied from 2.42 to 2.62 per grebe.hr. Open dots indicate the data from 4th, 17th and 18th September when flapping rates were close to 1.7 per grebe.hr. Every dot represent sample sizes of at least 100 grebe-minutes (maximum of 1692). Only the measurements made between 8 and 17 hr M.E.T. were used in the subsequent analyses.

growth (see Pimm 1976 for method). Since the growth rate of primaries is constant through most of the growth period, each moult phase will take about a third of the total moult duration. Values of either 5 days/phase (maximum estimated growth rate) or of 7 days/phase (average estimated growth rate) will be used below.

The moult composition of the population present is only accurately reflected by the composition of the moult phase samples, if birds in different moult phases have the same frequencies of wing-flapping bouts. If not, the percentages of birds in active wing-moult will either be over- or under-estimated. To find out, the daily average frequencies of wing-flapping bouts were plotted against the percentages of birds definitely in wing-moult (i.e. phases 1 and 2). Since an extraordinary amount of wing-flapping occurred in the early morning and early evening (Figure 5), only observations on wing-flapping bouts and wing-moult phases made between 9 and 17 hrs M.E.T. were included in the analysis (cf. Table 1 for actual data).

Table 1. Percentage of grebes in apparent wing-moult and wing-flap bout frequencies.

Date*	Number of grebe-min	Bouts/hr	Total No. of flapping grebes seen	Percentage moult ph.1	Percentage moult ph.2	Percentage moult ph.3
28.7	1050	0.69	79	4%	0%	96%
7.8	642	1.78	92	37%	0%	63%
13.8	360	1.67	135	16%	17%	67%
17.8	943	2.42	165	64%	20%	16%
23.8	3867	2.62	316	42%	35%	23%
28.8	1395	2.54	69	49%	32%	19%
4.9	3724	1.66	141	24%	28%	48%
17 & 18.9	12765	1.65	534	7%	18%	66%
30.9	4558	0.63	77	1%	13%	86%
15.10	4610	0.42	62	0%	3%	97%

*All 1986 except 28.7

Figure 6 shows the strong ($r=0.95$) correlation between the percentage of wing-moulting grebes and the frequency of wing-flapping bouts. A stepwise multiple regression analysis (Nie *et al.* 1975) showed that the percentage of birds in phase 1 contributed exactly as much to an increase in the frequency of wing-flapping bouts as the percentage of birds in phase 2 (the regression coefficients for both are 0.024, $r^2=0.89$, intercept=0.611, with no differences between regressions when either the percentages of phase 1 or phase 2 are entered first). Since at a theoretical 0% birds in wing-moult (i.e. intercept), the wing-flapping rate is 0.6 bouts/grebe.hr, and at a theoretical 100% 3.0 bouts/grebe.hr, birds in moult phase 1 and 2 would be predicted to flap their wings no less than $3/0.6 = 5$ times as frequently as birds in phase 3. However, there are reasons to think this is an overestimate.

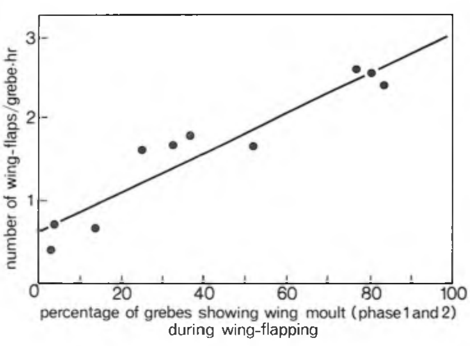

Figure 6. The correlation between the percentage of grebes showing wing-moult (moult phases 1 and 2) and the frequency of wing-flapping bouts of Great Crested Grebes. The heavy line represents the best fit ($y=0.024\,x+0.61$, $r^2=0.89$, $P<0.0001$).

In the field it was obvious that when one grebe was wing-flapping, it was likely that nearby grebes would also start wing-flapping. Sometimes, waves of wing-flapping could be seen moving through the rafts of grebes. Wing-flapping (like yawning in humans) can therefore be regarded as a socially facilitating behaviour. Wing-moulting individuals, being more prone to flap the wings anyway, would be particularly susceptible to such facilitation, but since only the first in a wave could be checked, the higher the percentages of moulting birds, the more these percentages are underestimated. While it is certain that moulting grebes flap their wings more often than non-moulting grebes, it is not yet possible to say exactly by how much. The factors 5, 2.5 and zero are used below as different assumptions for the increase in wing-flapping rates of moulting compared to non-moulting grebes.

To calculate population turnover under these different assumptions, the numbers present and the proportions of birds in different moult phases were tabled for each day. For the days between those on which the data presented in Figure 4 were collected, the figures were linearly interpolated. The tables were then divided in either 5 or 7 day periods (starting on 1st August), and the number of birds in the moult phases 1 and 2 calculated for each day, under different assumptions for relative wing-flap bout frequencies. Since the duration of moult phases 1 and 2 is assumed to be the same (i.e. each of 5 or 7 days), the difference between the estimated number of grebes in phase 1 in period 1 (n_1) and phase 2 in period 2 (n_2), yields an estimate of the number of grebes that moved away from the study area between periods 1 and 2 (if $n_2 < n_1$), or immigrated into the area (if $n_2 > n_1$). For similar reasons, the numbers of grebes in moult phases 1 and 2 in the different periods can be summed over the whole season to get an estimate of the total numbers of individuals which had occurred near the Mokkebank in the two moult phases.

The estimates of the number of grebes starting wing-moult near the Mokkebank in 1985 and 1986 varies from 3,400–24,000 and from 5,000–35,300 respectively, depending on the assumptions made (Table 2). Whereas the estimates assuming no difference in wing-flap bout frequencies of moulting and non-moulting birds are clearly too high, the estimates based on a factorial difference of 5 are probably too low, for the reasons outlined above. It is suggested that the estimates based on a factorial difference of 2.5, and a moult duration of 5 days/phase (underlined in Table 2), are of the right order.

Using these last assumptions, the values of several population parameters of the wing-moulting Great Crested Grebe population near the Mokkebank may now be examined (Table 3). The differences between the years 1985 and 1986 are due to much lower average numbers of both adults and juveniles present in 1985, and a comparable difference in the total number of grebes recorded in wing-moult. The large temporary decline in numbers in the end of August and early September 1985 resulted in much lower numbers recorded in phase 2 than in phase 1 in 1985, and in a concurrent high value for the emigration of birds having just started wing-moult. In 1986, total numbers recorded in phase 1 and phase 2 differ little, and the estimates of immigration and emigration after phase 1 are relatively low. It is remarkable that both in 1985 and in 1986 the total number of grebes recorded in wing-moult is almost twice the average number that was present, but is close to the maximum number that occurred during the season.

Table 2. Estimates of numbers of grebes starting wing-moult near the Mokkebank in 1985 and 1986, under different assumptions for length of moulting period and relative wing-flapping bout frequencies. The underlined figures are probably closest to reality.

Year	Length of moulting period	Assumptions: Birds in moult flap 5 times as frequently	Birds in moult flap 2.5 times as frequently	No difference between flapping bout rates in moulting and non-moulting birds
1985	21 days (7 days/phase)	3400	6900	17200
	15 days (5 days/phase)	4800	9600	24000
1986	21 days (7 days/phase)	5000	10000	25200
	15 days (5 days/phase	7000	14000	35300

Table 3. Population parameters of wing-moulting Great Crested Grebes. To calculate the average total number present, only counts made between 6 August and 15 October were used. The number of juveniles was estimated from the average proportion of juveniles in special scan-samples made between 6 August and 15 September of each year. The number of grebes in different phases were calculated under the assumptions of a 2.5 times increase in wing-flap bout frequencies and a phase duration of 5 days.

Category	Year of observation 1985	1986
Average total number present	4900	11300
Average number of juveniles	100	2000
Number starting wing-moult (phase 1) at Mokkebank (a)	9600	14100
Number starting wing-moult elsewhere (b)	1300	3000
Number emigrated after starting wing-moult	5700	3400
Number recorded in phase 2	5300	13700
Total number recorded in wing-moult (a + b)	10900	17100
Maximum number recorded	8000	18000

Discussion

Clearly, there is considerable turnover in the population of wing-moulting Great Crested Grebes near the Mokkebank. This means that the moulting area is of importance to larger numbers of birds than was apparent from counts of total numbers. In the absence of accurate data on the effects of the phase of moult and of facilitation by conspecifics on relative wing-flap bout frequencies, the turnover-estimates can still only be given as a range. However, the use of wing-moult as a temporary marker of cohorts of birds has certainly potential for studies on waterbird-populations in general. This is especially so for species which remain on open and deep water during moult (Jepsen 1973; van Impe 1978; van der Wal and Zomerdijk 1979; Winkler and Cooper 1986), and therefore cannot easily be captured by rounding up to mark and examine in the hand (Owen and Ogilvie 1979; Boyd and Maltby 1980). It should also be possible to use the method on species with more secretive moulting habits. For example, surface feeding ducks, which hide in freshwater reedbeds during wing-moult, are often visible (from blinds) for part of the day when they are feeding on open lagoons. However, in order to reduce the number of assumptions affecting the present estimates, the pertinent factors should be studied in captivity.

Observations on moult phase composition in wing-flapping birds may still yield invaluable qualitative data on the timing of moult in most species, and the differences between the timing of moult of the sexes in sexually dimorphic species (diving ducks, seaducks and sawbills). The only requirements are a good viewpoint and a telescope!

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Summary

Flapping the wings is a common comfort behaviour in waterbirds. It is easy to see whether a bird is in wing-moult or not, and to see the extent of feather renewal. Since each moult phase takes a definitive number of days, wing-moulting waterbirds are naturally marked in successive cohorts. Combining observations on moult phase with data on the numbers present, it is possible to calculate minimum rates of emigration and immigration of moulting individuals (turnover). In August-October 1985 and 1986 the method was applied on a population of Great Crested Grebes *Podiceps cristatus* moulting in Lake IJsselmeer, The Netherlands. Only the possible range in the extent of population turnover could be determined. In both study years, the best approximation of the total numbers of grebes that had been present while in wing-moult, was almost twice the average number recorded. With more information on the variability in wing-flapping bout rates, the method has great potential for studies of moulting waterbirds in sites or habitats where they are difficult to study otherwise.

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