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Authors: Abt, Kai, and Konter, André

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Survival rates of adult European grebes (Podicipedidae)

Kai Abt[1] & André Konter[2,*]

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Ring recoveries of dead individuals from all over Europe and covering a period of 57 years were collected to study survival of Great Crested *Podiceps cristatus* (*n* = 433), Black-necked *P. nigricollis* (*n* = 95) and Little Grebes *Tachybaptus ruficollis* (*n* = 295). Survival rates of adult birds were estimated by fitting simple mark–recapture models via maximum-likelihood. Realizing that the samples were extremely heterogeneous and possibly biased, it was further investigated how the survival data conformed to information from literature on fledging success, age at first breeding, and long-term population trends. In the Great Crested Grebe, ring recoveries were biased towards young birds, as indicated by a marked, untypical increase in apparent survival after the age of 3 years. Also, the whole-sample estimate of 0.66 was too low to match the other demographic parameters. The survival rate of 0.75 (95% CI 0.69–0.80) estimated for birds of 4 years and older conformed well with the breeding performance established for Great Crested Grebes and is thus considered as a realistic estimate for adult birds. The survival rate estimate of 0.63 (95% CI 0.55–0.70) for the Black-necked Grebe seemed a slight underestimate given estimates for the other demographic parameters. Apart from a possible, albeit undetected, sample bias towards younger birds, some influence of ring loss cannot be excluded, because in contrast to the other two species, the Black-necked Grebe sample contained a high proportion of aluminium rings. The survival rate of Little Grebe was estimated at 0.60 (95% CI: 0.55–0.64), which corresponded well with other demographic data.

Key words: population dynamics, survival, ring recoveries, mark–recapture, *Podiceps cristatus, Podiceps nigricollis, Tachybaptus ruficollis*

[1]Wildlife Consulting, Samwerstr. 32, 24118 Kiel, Germany;
[2]45, rue des Romains L-6478 Echternach; collaborator of the Museum of Natural History, Luxembourg, L-2345 Luxembourg;
*corresponding author (podiceps@pt.lu)

INTRODUCTION

Changes in closed avian population sizes are determined by survival and reproduction rates (Nichols 1991). Measures of both are often desired by wildlife conservationists, particularly when changes in stock size are difficult to observe directly (Caughley 1977, Eichholz & Sedinger 2007). They may also be used as baseline figures in environmental impact studies that aim at predicting losses in wildlife populations through anthropogenic causes (Morrison *et al.* 1998, Dierschke *et al.* 2003, Sperduto *et al.* 2003). In birds, survival can be measured either from live recaptures of marked individuals or from ring recoveries of birds recorded as dead (Clobert & Lebreton 1991). A powerful methodology has been developed for the analysis of such data obtained under various conditions (White & Burnham 1999). Grebes Podicipedidae, however, are difficult to catch, which makes live recapture programs impracticable, and grebe ring returns are very scarce. Attempts to estimate survival have been made for the Great Crested Grebe *Podiceps cristatus* (Fuchs 1982, van der Poel 1984), but these were based on small sample sizes. Aiming to estimate survival rates for Great Crested *Podiceps cristatus*, Black-necked *P. nigricollis*, and Little Grebe *Tachybaptus ruficollis*, we collected ring recovery records from many parts of Europe compiled over a period of 57 years.

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The heterogeneous nature of the ring recoveries, and potential bias therein, may complicate their interpretation (e.g. Botkin & Miller 1974, Fuchs 1982). To check the accuracy of the survival estimates, we constructed a simple population model that included independent information on fledging success, age at first breeding, and long-term population trends as derived from literature.

METHODS

Inference from ring recoveries

Upon request, we received records on ringing and recoveries for all five European grebe species from 25 ringing centres throughout Europe (see Acknowledgements). Samples of Red-necked *P. grisegena*, and Horned Grebes *P. auritus* were too small for analysis. To estimate survival rates we only used dead recoveries, which formed the majority of the records. Live-recapture data from local ringing programs were screened for birds of old age. Among dead recoveries, 45% of Great Crested Grebes and 39% of Little Grebes appeared to be victims of an anthropogenic source, mainly by drowning in fishing nets and hunting (Table 1). However, in about half of the cases no cause of death had been reported, and it is likely that many of these had died by anthropogenic causes as rings of birds starved or killed by predators must have a low chance of recovery. A priori, this needs not be a problem, provided that birds of every age and sub-population are equally affected by anthropogenic mortality agents. In reality, however, it is necessary to consider that samples obtained in this way may be significantly biased.

We analysed ring recovery data of birds that had survived at least their first winter, i.e. birds found dead from 1 May of their second calendar year on and that had been reported to be dead for no longer than a few weeks. In a few instances, no remains of the bird were found together with the ring. The corresponding data were not included in the analysis because of a possibly long time lag between death of the bird and ring recovery. We defined year of death k from 1 May of calendar year k to 30 April of calendar year k + 1. Age at death was then given by year of death minus presumed year of hatching. The latter in turn was inferred from age at ringing, as known from EURING age codes (Speek *et al.* 2001) indicated by the ringers (Table 2). Because information from codes 0, 2, 4, and 6 is not precise, we made the following assumptions: birds with code 0 and 2 were regarded to be in their second calendar year when ringed before the month of peak occurrence of pulli, i.e. July in Great Crested and June in Little Grebe. When ringed in or after that month, however, they were regarded as fledglings of the year. Birds with code 4 were treated as if they had been ringed in their second calendar year. To simplify modelling, this was also done with the very few birds with code 6, that theoretically could be classified as being at least in their third calendar year. As the year of hatching was not definitely known in 58% of the birds, we suspect that 'age' referred to in the following is an underestimation of the true age.

From the obtained frequencies of deaths at different 'ages', the survival rates from the second calendar year

Table 1. Reported causes of death of dead recovered grebes (as % of total numbers).

	Great Crested Grebe (n = 433)	Black-necked Grebe (n = 95)	Little Grebe (n = 295)
Dead, unknown cause	48.3	32.6	52.9
Shot	17.6	34.7	27.5
Drowned in fishing net	21.2	14.7	0.7
Fatal accident	2.8	7.4	8.1
Pollution	3.5	3.2	2.4
Natural cause	4.4	4.2	5.8
Predation	2.3	3.2	2.7

Table 2. EURING age code and distribution of dead recovered grebes (as % of total numbers).

Code		Great Crested Grebe (n = 433)	Black-necked Grebe (n = 95)	Little Grebe (n = 295)
0	Age unknown or not indicated	2.3	1.1	3.4
1	Pullus, unable to fly	25.9	26.3	5.8
2	Fully grown bird, able to fly	11.5	9.5	41.0
3	Fully grown bird, hatched in this calendar year	15.7	12.6	14.2
4	Fully grown bird, hatched before this calendar year	39.0	30.5	28.8
5	Fully grown bird in the second calendar year	2.5	5.3	4.4
6	Fully grown bird in the third calendar year at least	3.0	14.7	2.4

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on was estimated using methodology outlined by White & Burnham (1999). We employed a simple, holistic ring recovery model that omits the (unknown) cohort sizes of birds ringed and assumes adult survival to be constant with age, year, and location. The probability that a bird is found dead in a particular year can be defined as

$$P_{xy} = S^{x-1} (1 - S) (1 - S^{y})^{-1},$$

where S is survival rate, x = 1, 2, 3, … is 'age' at death, and y = 1, 2, 3, … is the number of years at risk, i.e. the last year of the sampling period (2000 in Great Crested, 2002 in Black-necked, 1998 in Little Grebe) minus assumed year of hatching. The term S^{y} denotes the probability that a bird hatched in year y–1 (and thus one year old in year y) is still alive after the last year of the sampling period. It approximates zero as y becomes larger. The parameter S was determined by maximum-likelihood estimation, i.e. by fitting S such as to maximize the log-likelihood term

$$\text{Log } L = \sum N_{xy} \text{ Log } P_{xy},$$

where N_{xy} is the number of grebes ringed in year y and found in year x. Confidence limits of S were found by the curvature method, as described in Schrago (2006), based on angular-transformed values.

In addition to the above model, which assumes constant survival throughout all age-classes, we employed a design allowing for a change in survival rate at a given age, i.e. models with two age groups. This was done in order to detect possible heterogeneity in the data that might lead to biased results from the model without age groups. The age groups distinguished varied from 2 until the highest figure for which at least 20 birds were left in the older group. Model selection was based on Akaikes's information criterion (AIC), a function of the likelihood and the number of model parameters. Based on the parsimony principle, a lower AIC value indicates better model fit at limited complexity (Burnham & Anderson 1998). AIC differences of >2 were considered noteworthy.

Inference from fledging rates

Establishing survival from fledging rates requires knowledge of approximate population trends. European Great Crested Grebes mainly increased during the second half of the 20th century, with data from The Netherlands, UK, France, Belgium, Estonia, Norway and Fennoscandia suggesting an average growth rate of 4–5% per year over at least 3–4 decades (Bauer & Berthold 1996, O'Donnell & Fjeldså 1997, Snow & Perrins 1998, BirdLife International 2000, 2004, Bauer *et al.* 2005). There was a moderate decline in Western Europe during the 1990s (BirdLife International 2004, Bauer *et al.* 2005), which is, however, of minor importance because less than 7% of the ring recoveries for this species were from that decade. Population data for the Black-necked Grebe are less conclusive, although they similarly indicate an increase between 1960 and 1990 in Western and Central Europe, and, after 1990, local declines in some Eastern European countries (Bauer & Berthold 1996, O'Donnell & Fjeldså 1997, BirdLife International 2000, 2004). Little Grebe numbers remained stable, although undergoing considerable short-term fluctuations which relate to occasional high winter mortality (O'Donnell & Fjeldså 1997, BirdLife International 2004, Bauer *et al.* 2005). In our models, we assumed a stable population of the Little Grebe over the study period, which means that the finite rate of increase (λ) equals 1.00. For the other two species we considered both a stable stock and one that increases at 5% per year (λ = 1.05).

Information on the annual number of fledglings *per breeding pair* (F) was also obtained from literature. In the Great Crested Grebe, the broad average appears to be within 1.0–1.5 fledglings per breeding pair (Prinzinger 1979, Vlug 1983, Ulfvens 1988, Ulenaers & Dhondt 1991, Arratíbel *et al.* 1999, Konter 2004). Figures of 1.0–2.0 are considered for the Black-necked Grebe (Bandorf, Fiala, Knötzsch in Prinzinger 1979, Leibl & Zach 1992). Little Grebes have as many as 2.0–2.5 fledglings per breeding pair due to frequent second broods (Bandorf 1970, Hughes 1992, Dittberner 1996). Note that all mature birds are assumed to be part of the breeding population to which F refers.

In order to establish adult survival rate (S), which we assumed to be constant from age 1 onwards, we need to know the survival rate of fledglings (S_1), since

$$S + S_1\, 0.5\, F = \lambda.$$

Lacking knowledge of both survival rates, S_1 may be expressed as a function of S. We assumed that first-year mortality $(1 - S_1)$ is elevated by some factor k in relation to adult mortality (1 – S), i.e.

$$(1 - S_1) = k\, (1 - S),$$

with k supposedly being in the range of 1–2 (see Discussion). Finally, we took account of delayed breeding, thus the younger age classes may not be part of the

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breeding population which literature values of F refer to. Assuming that birds start breeding at some specific age f, the annual recruitment is proportional to S^{f-1}, rather than to S. Hence, we arrive at

$$S + S^{f-1} [1 - k (1 - S)] 0.5 F = \lambda.$$

If f assumes low naturals (1, 2) and λ equals 1, this can be solved for S by linear algebra. Otherwise, S must be found using Newton iterations.

According to Bandorf (1970) and Fjeldså (2004), Little Grebes generally breed from their second calendar-year onwards (i.e. f = 1). Great Crested Grebes may sometimes breed at the age of one year, but usually first breed at the age of two years (f = 2) (Simmons 1989, Vlug 1983, 1985, 2007). Black-necked Grebes are sexually mature in their second calendar-year (Prinzinger 1979), but common occurrence of non-breeders, presumably second-year birds, near colonies (Konter, unpubl.) suggest that f = 1.5 may be more adequate for the European nominate.

RESULTS

As indications of minimum longevity, recorded maximum ages of grebes are given in Table 3. Obviously, the Great Crested Grebe can exceed 20 years of age. No Black-necked Grebe older than 13 years was found, which must be seen in relation to the small overall number (37) of recovered birds ringed before 1989. As the oldest bird was shot, it could have grown older. A

Table 3. Recorded maximum ages of grebes from dead and live recaptures; individual numbers of live recaptures were 77 in Great Crested, 7 in Black-necked, and 131 in Little Grebe. See Table 2 for age codes.

Species	Ringing scheme	Age code	Ringing date	Recovery date	Age (years)	Circumstances
Great Crested Grebe	Spain	4	30.06.71	12.09.93	23	Dead for more than 1 week
	Russia	1	28.07.66	15.11.85	19	Freshly shot
Black-necked Grebe	Czech	4	08.06.65	03.08.77	13	Freshly shot
Little Grebe	UK	4	27.06.57	02.09.79	23	Ring found only
	Switzerland	4	22.10.56	25.02.73	17	Released alive

Table 4. Results of mark–recapture analysis of grebe dead recoveries; each row contains the results of a different model; the first, basic model (older age group = 1+) returns a single average survival rate for the entire sample, while the others assume a change of survival at a given age with survival rates for the two age groups; ΔAIC indicates how well a model explains the data as compared to the basic model, with negative values denoting better performance.

	Older age group	*N* in older age group	Survival rate (per year)	Survival rate of younger age group	ΔAIC
Great Crested Grebe	1+	272	0.66	-	-
	2+	161	0.69	0.59	–5.4
	3+	102	0.72	0.61	–7.8
	4+	66	0.75	0.62	–10.2
	5+	49	0.75	0.63	–5.6
	6+	36	0.75	0.64	–3.1
	7+	26	0.77	0.64	–3.1
Black-necked Grebe	1+	70	0.63	-	-
	2+	45	0.59	0.67	0.9
	3+	20	0.69	0.60	0.5
Little Grebe	1+	168	0.60	-	-
	2+	92	0.63	0.55	–0.2
	3+	56	0.64	0.57	0.5
	4+	38	0.61	0.59	1.9

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Little Grebe was released alive when at least 17 years old. The oldest record referred to a 23-year old bird, but as no remains were found this record is questionable.

The basic mark–recapture model yielded average adult survival rates of 0.66 (95%-CI 0.62–0.69), 0.63 (0.55–0.70), and 0.60 (0.55–0.64) in Great Crested, Black-necked, and Little Grebe, respectively (Table 4). In the Great Crested Grebe, however, models allowing for a change of survival rate with age provided a better description of the data. Model selection indicated a strong support for the model with a shift in survival at age 4. The survival estimate for the older group increased with the age of splitting until a maximum value was attained at age 4. Survival of Great Crested Grebes of at least 4 years of age was estimated at 0.75 (95%-CI: 0.69–0.80). In the other two species, there is no statistical support for a shift in survival with age.

Adult survival rates inferred from the simple population model are given in Table 5. The observed population increase of 5% per year ($\lambda = 1.05$) in Great Crested and Black-necked Grebe requires that survival rates are 0.02–0.03 higher than for a stable population. Changes in k make little difference when $f = 2$ and $F \leq 1.5$ as in the case of the Great Crested Grebe. In the Little Grebe, in contrast, where $f = 1$ and $F = 2.5$, k has a considerable influence on the resulting survival rate. In the Great Crested Grebe, the survival estimate of 0.66 from the basic mark–recapture model implies equally high survival during the first year ($k = 1.0$) and more than 1.5 fledglings per pair (Table 5). With moderately elevated first-year mortality ($1.0 < k < 1.5$) and less than 1.5 fledglings, however, adult survival must be substantially higher, i.e. at least of the magnitude found in birds of 4 years and older (0.75), to maintain a stable or increasing population. In the Black-necked Grebe, similarly, the mark–recapture estimate of 0.63 requires either equally high first-year survival and about 1.5 fledglings per pair, or as many as 2 fledglings with moderately lower first-year survival ($1.0 < k < 1.5$). The situation in the Little Grebe is exceptional in that F is relatively well-known, and S is particularly sensitive to changes in k. The survival rate estimate of 0.60 conforms to a moderately elevated first-year mortality ($k \sim 1.5$), while F may be 2.0–2.5 fledglings per pair.

DISCUSSION

The goal of this investigation was to establish average survival rates of European grebes in the second half of the 20th century. Compared to other mark–recapture studies, we pooled records collected over a very long sampling period and from a large area. This was necessary to obtain reasonable sample sizes, given the limited number of ring recoveries in each grebe species. Also, the samples are clearly biased towards certain countries (particularly The Netherlands and Switzerland), but as long-term population trends in grebes seem to have been similar over large parts of the

Table 5. Annual survival rates of adult grebes calculated from age at first breeding (f), fledging rates (F), population rates of increase (λ), and ratio between first-year and annual adult mortality (k).

Species	Age at first breeding (f)	Fledglings per pair (F)	Population rate of increase (λ)	Adult survival rate at ratio (k) of first-year vs. annual adult mortality		
				k = 1.0	k = 1.5	k = 2.0
Great Crested Grebe	2	1.0	1.05	0.76	0.78	0.80
			1.00	0.73	0.76	0.78
		1.5	1.05	0.69	0.73	0.76
			1.00	0.67	0.71	0.74
Black-necked Grebe	1.5	1.0	1.05	0.73	0.77	0.79
			1.00	0.70	0.74	0.77
		1.5	1.05	0.65	0.70	0.74
			1.00	0.63	0.68	0.72
		2.0	1.05	0.59	0.66	0.71
			1.00	0.57	0.64	0.69
Little Grebe	1	2.0	1.00	0.50	0.60	0.67
		2.5	1.00	0.44	0.57	0.64

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species' range (O'Donnell & Fjeldså 1997, BirdLife International 2004, Bauer *et al.* 2005), the results may be applicable to much of the European range.

Because our ring recoveries originate mainly from anthropogenic mortality, certain bias in the samples was to be expected. In particular, younger birds may be overrepresented relative to older, more experienced individuals. Apparent consequences thereof are discussed farther below. Another possible source of bias is ring loss (Botkin & Miller 1974, Nelson *et al.* 1980). For North American Eared Grebes *P. nigricollis californicus* staging at the highly saline Mono Lake, California, aluminium ring loss begins within 3–4 years and becomes a serious problem within 5–6 years from ringing (Jehl 1990). This is of particular relevance in the Black-necked Grebe, because in this species most rings recovered were from Eastern European schemes, which used aluminium rings until recently. In contrast, the UK, The Netherlands and Switzerland introduced stainless steel rings in the 1960s, followed by Finland and Germany between 1968 and the early 1980s (J. Clark, M. Kestenholz, J. Haapala, W. Foken, W. Fiedler, R. Wassenaar, S. Kharitonov, J. Cepák, pers. comm.). Therefore, about half of our Great Crested and Little Grebe samples consist of steel rings, giving little reason for concern about substantial influence of ring loss in our results. Moreover, significant ring loss typically leads to an apparent decrease of survival with age (Nelson *et al.* 1980), a pattern not observed in our analysis of ring recoveries.

As to the indirect assessment of survival rates, inference from fledging success may give rise to biased results as well. For instance, Vlug's (1983) average family size of 1.1 for Great Crested Grebes, based on 19 561 breeding pairs from various European populations, includes chicks of various age classes. This may have overestimated fledging success. On the other hand, the figure does not account for second and third broods. As a consequence, it may even represent a conservative estimate of fledging success. Furthermore, published fledging rates may not be representative for the entire period from which ring recoveries were obtained. However, recalling that populations remained broadly stable (Little Grebe) or increased for most of the sampling period (Great Crested Grebe), significant change of population parameters may not be inferred. As we considered a range of F-values, possible changes of productivity are unlikely to be an important source of error in the calculations. Among the parameters considered, the least-known was first-year mortality, which we introduced in the form of the artificial parameter k. Assuming some specific ratio of first-year vs. adult annual mortality has no theoretical justification, but it makes some sense from an empirical point of view. For the Great Crested Grebe, Fuchs (1982) estimated 41% first-year and 30% adult mortality in a decreasing population in Switzerland, yielding a k-value of 1.37. In divers *Gavia* spp., which ecologically are to some extent comparable to grebes, but have fewer offspring ($F \sim 0.55$) and presumably higher adult survival ($S \sim 0.88$; Sperduto *et al.* 2003), k equals about 2. Higher values of k seem unlikely for grebes because they imply either very high adult survival rates, like in loons and many seabirds, or higher offspring numbers than those observed. Some small- to medium-sized raptors, i.e. Sparrowhawk *Accipiter nisus*, Goshawk *Accipiter gentilis*, and Peregrine *Falco peregrinus*, have k-values between 1.5 and 2.0, while, roughly comparable to grebes, adult survival rates are in the range of 0.65–0.80, and fledging rates (including unsuccessful pairs) within 1.5–3.0 (Newton & Rothery 1998, Snow & Perrins 1998, Nielsen & Drachmann 2003, Robinson 2005).

In the Great Crested Grebe, ring recoveries indicated a substantially lower survival rate of 1–3-year-old individuals (0.62), as compared to birds of 4 years and older (0.75). For three reasons, this is almost certainly an artefact, resulting from overrepresentation of young birds in the samples. First, low juvenile survival (0.62 vs. 0.75 in 'adults') is very unlikely to extend until age 3 in a species that starts to breed at age 2. In general, a major change of survival after the first year of life is untypical in birds (Caughley 1977). Second, the average figure of 0.66 obtained from the entire sample is too low to allow for a most likely elevated mortality during the first year (Melde 1973, Fuchs 1982, van der Poel 1984). Finally, it implies an average fledging rate of more than 1.5, which compares poorly to Vlug's (1983) mean family size of 1.1. Even if the latter was a slight underestimate, because it disregards multiple broods, the survival rate estimate obtained from the birds older than 4 years seems more realistic. Therefore, we consider a survival rate of 0.75 as a plausible value for adult Great Crested Grebes.

In the Black-necked Grebe, in contrast, there is no indication of a significant change of survival at an unusual age. However, this does not necessarily imply a representative sample, but it could be due to the relatively small number of records. At least, our estimate of 0.63 is in line with the literature, as Sperduto *et al.* (2003), summarizing a number of references, quote a similar value of 0.62 for adult North American Horned and Red-necked Grebes. However, these authors also assume high productivity ($f = 1$, $F = 1.82$) and a high fledgling survival (0.60). For the European Black-

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necked Grebe, data on fledging success are relatively scarce, but there is little support for an average as high as 1.5–2.0 (Prinzinger 1979, Leibl & Zach 1992). Moreover, a lack of higher mortality during the first year seems counterintuitive, considering the evidence in both the Great Crested and the Little Grebe (see below), and many other European bird species (Snow & Perrins 1998, Robinson 2005). Therefore, the survival rate of adult Black-necked Grebes in stable or increasing populations may rather be close to 0.70, or even higher. Ring loss and bias towards young birds, both undetected due to the limited statistical power of the sample, are possible reasons why our estimate is lower. In any case, uncertainty about population parameters remains high in this species, which could partly be a consequence of high variability in time, as suggested from fluctuations in population size (O'Donnell & Fjeldså 1997). For North American Eared Grebes, Jehl *et al.* (2002), referring to Cullen *et al.* (1999), suggest a survival rate as high as 0.95 in both adults and fledglings between 1998 and 2000. However, this figure refers to a two-year period in which the grebe population doubled, recovering from a catastrophic decline related to an El Niño event. The long-term average survival rate, including periods of decline, will be lower. Assuming that population numbers fluctuate around some stable mean, and accepting values of further vital parameters as suggested by the authors ($f = 1$, $F = 0.8$, $k = 1$), the average survival rate of the North American sub-species would in fact be down to 0.71.

In the Little Grebe, there is also no indication of bias in the mark–recapture sample. Given the high productivity of the species, our survival rate estimate of 0.60, corresponding to a k-value of about 1.5, is realistic. As in the Black-necked Grebe, the result summarizes both population crashes and recovery periods, and should thus represent the long-term mean survival rate. Referring to the large short-term fluctuations, Vlug (2005, 2007) postulated low survival of Little Grebes and suggested a key role of suitable winter habitat. From the fact that both juveniles and adults face at least occasional high winter mortality, one may expect that the survival rates of both age groups do not differ too much, and, thus, k tends to be lower than in other grebes. From our results, however, figures lower than 1.5 seem unlikely even for the Little Grebe. As there also is little support for k ranging much higher in any of the species, values around 1.5 may be generally adequate for European grebes.

Looking at adult survival rates of other non-pelagic water birds, we find that many estimates are in the range of 0.60–0.75 suggested here for European grebes, e.g. 0.61–0.75 for Gadwall *Anas strepera* (Giudice 2003, Szymczak & Rexstad 1991), 0.66 for Hooded Merganser *Lophodytes cucullatus*, 0.63 for Wood Duck *Aix sponsa* (Dugger *et al.* 1999), 0.65 for Common Pochard *Aythya ferina*, and 0.71 for Tufted Duck *Aythya fuligula* (Blums *et al.* 1996). Of course, anatids have more offspring than grebes, implying that fledgling survival will be lower.

Obviously, animal survival rate estimates are easily under-estimated for a number of reasons. As we have shown, however, severely biased results can be identified if information on reproduction and population trends of the species is utilized. We believe that wildlife population research could benefit from a more common use of this approach, in a way that obtained estimates be discussed more critically to avoid unrealistic values. For instance, Sperduto *et al.* (2003) list first-year and adult survival rate, fledging rate, and age of first breeding from various references for seven taxa of marine birds, and use these figures to estimate population losses from the 'North Cape' oil spill off Rhode Island in 1996. Employing the population model above reveals that the parameters assumed by the authors for Red-breasted Merganser *Mergus serrator*, Common Goldeneye *Bucephala clangula* and Common Eider *Somateria mollissima* would lead to quasi-extinction (i.e. a 90% population loss) within 9–11 years. As no such dramatic declines have been reported, either fledging or, more likely, survival rates must be too low. We believe it may be useful in studies of animal survival to perform some test of plausibility, based on information on stock trends and reproduction. Moreover, as the latter parameters are often easier to establish, indirect estimation of survival rates by means of simple population models may be the best solution, particularly if direct estimates from marked animals are missing or appear unreliable.

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SAMENVATTING

Om de overleving van futen (Podicipedidae) te schatten werden de ringvondsten uit een groot aantal Europese landen verzameld. Voor de Fuut *Podiceps cristatus* (433 terugmeldingen), Geoorde Fuut *P. nigricollis* (95) en de Dodaars *Tachybaptus ruficollis* (295) was het aantal terugmeldingen (verzameld over een tijdsbestek van 57 jaren) voldoende voor een dergelijke schatting. Om te kijken of de overlevingsschattingen realistisch waren, werd de overleving ook geschat aan de hand van een simpel populatiemodel met literatuurgegevens over populatiegroei, jongenproductie en de leeftijd waarop de vogels met broeden beginnen. Bij de Fuut bleek de geschatte jaarlijkse overleving na het derde levensjaar toe te nemen. Een dergelijke trend lijkt onwaarschijnlijk en is waarschijnlijk een gevolg van het feit dat ringvondsten van jonge vogels (om welke reden ook) oververtegenwoordigd waren. Bovendien leverden de terugmeldingen een schatting op van een overleving van 0,66. Dit bleek te laag om de waargenomen groei van de Europese populatie te verklaren. Een schatting van de overleving op grond van terugmeldingen van Futen van 4 jaar en ouder (0,75) bleek goed in overeenstemming te brengen met het populatiemodel. De ringgegevens van de Geoorde Fuut wezen op een overlevingskans van 0,63. Dit was een lichte onderschatting in vergelijking met het populatiemodel. Een onderschatting van de overleving kan veroorzaakt zijn door het feit dat veel van de Geoorde Futen waren geringd met aluminiumringen, die een beperktere levensduur hebben dan stalen ringen. De overlevingskans van de Dodaars werd geschat op 0,60. Dit kwam goed overeen met de uitkomsten van het populatiemodel. (DH)

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