Migration and survival of Black-headed Gulls *Larus ridibundus* ringed as chicks in Denmark

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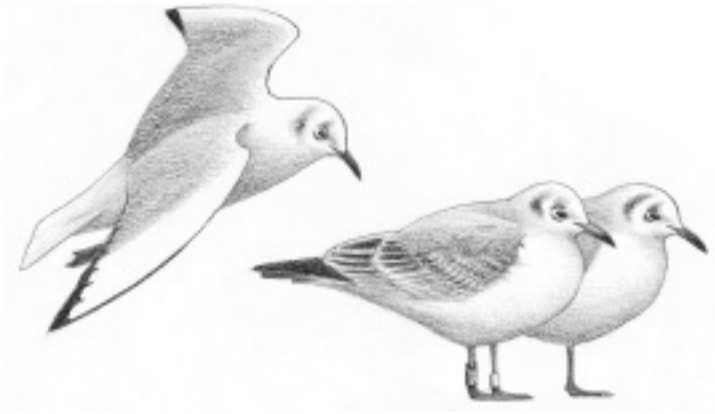

(Med et dansk resumé: Træk og overlevelse af Hættemåger Larus ridibundus *ringmærket som unger i Danmark)*

Introduction

The Black-headed Gull *Larus ridibundus* is the most abundant gull species breeding in Denmark (Christensen 1990). Many chicks have been ringed every decade since the 1930s, which have resulted in a large number of recoveries. During this period, the Danish population has shown great fluctuations with an increase until the 1980s (Christensen 1990) followed by a steep decline (Heldbjerg 2001); the Black-headed Gull is now listed in the 1997 Yellow List (Stoltze & Pihl 1998) as a species requiring special attention. In order to identify the reasons for the decline, it is important to understand the migratory movements of the species. Ringing recoveries have previously been analysed by Skovgaard (1923), Pedersen (1924), Tåning (1944), Salomonsen (1953) and most recently by Andersen-Harild (1971). Since then the number of recoveries has increased almost tenfold, which makes it possible to analyse the migration in greater detail.

This paper presents the first survival analyses for Danish Black-headed Gulls, a parameter fundamental for understanding changes in population size.

Material and methods

The study was based on 1635 ringing recoveries of Black-headed Gulls ringed as chicks in Denmark and reported to the Zoological Museum before 26 March 1999. Excluded were resightings of live birds, birds recovered as shot, birds recovered less than 10 km from the ringing site and recoveries with uncertain recovery dates (more than 10 days) or where only the ring was found. Aluminium rings were used until 1972 and thereafter replaced by steel rings. The durability of these on Black-headed Gulls was at least 10-15 years for the aluminium-type and life-long for the steel-type (K.T. Petersen pers. comm.). Thus loss of rings is not judged to be of any importance when estimating the mortality rate.

Whether shot and resighted birds should be included or not in an analysis of ringing data is a difficult decision; the risk of bias in collection of these data in time and space has to be weighed against the loss of data.

Since most Black-headed Gulls first breed in their third year (Flegg & Cox 1972), first-year (1y), second-year (2y) and adults (3y+) were considered separately. Age classes were defined from 1 July in any one year since this is when most chicks fledge (Flegg & Cox 1975).

I used 10-day periods to examine the beginning of the autumn migration and the end of the spring migration for all age-classes.

Vector addition (Batschelet 1981) was used to calculate a mean angle of orientation based on

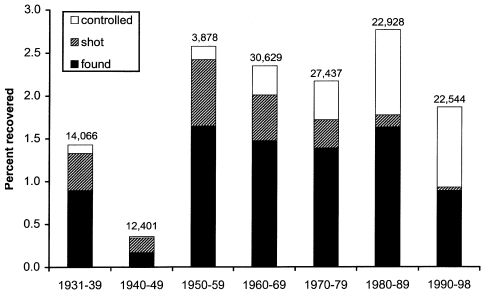

Fig. 1. Recovery percentage of Black-headed Gulls ringed as chicks in Denmark and controlled, shot and found dead, respectively, per decade. The total number of ringings in each time period is shown at the top of each column.
Genmeldingsprocent pr årti for Hættemåger ringmærket i Danmark som unger og genmeldt som henholdsvis aflæst, skudt og fundet død. Antallet af mærkninger i hver periode ses over søjlerne.

individual recovery directions. The mean vector length r, ranging between 0 and 1, measures the concentration of the circular distribution, the significance levels of which were tested using the Rayleigh test (Batschelet 1981). Differences in median distances were tested using the Mann-Whitney U-test; correlations were tested by Spearman Rank test; differences in annual survival rate were tested using linear regression and runs test**.**

The suggestions of Andersen-Harild (1971) about the wintering area for Danish Black-headed Gulls, that there was a difference for fledglings from different regions in Denmark and that there was a change from the 1930s to 1960s, were extended to the 1990s and reanalysed using this material. For that purpose the wintering area was divided into the geographical regions, 1) Denmark, 2) Great Britain, 3) Netherlands, Belgium and Germany, and 4) France and further south.

Lack's classical model (e.g. Lack & Schifferli 1948) was used to estimate survival through the first year and the modification of Haldane (1955) to estimate annual survival of older ('adult') birds. To ascertain that the lower survival rate of immatures had risen to the adult level before the age of one year, I looked at the ratio of first-year recoveries to total recoveries at a monthly basis (cf. Lack & Schifferli 1948, Lack 1951, Peach et al. 1994). Only recoveries considered to be complete (birds ringed prior to 1983) were included in the estimate of the first-year survival.

Results

Recoveries. A total of 133 883 Black-headed Gull chicks ringed before the end of 1998 resulted in 2717 recoveries (2%). 60% were from birds found dead, 25% from resightings and 15% from shot birds (Fig. 1). There was no trend in recovery rate for birds found dead (five-year periods 1931-1995 with 1941-50 excluded; $r_S = 0.35$, $p = 0.30$).

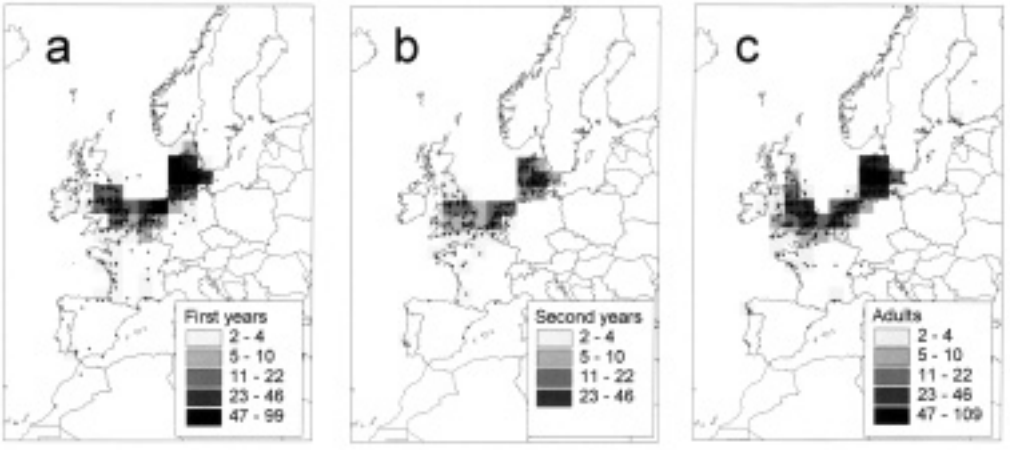

Fig. 2. Map of recoveries of Black-headed Gulls ringed as chicks in Denmark and found dead as a) first-year birds (n = 754), b) second-year birds (n = 240), and c) adults (n = 641). Points mark single recoveries, and the degree of grey tone denotes the number of recoveries per square.
Kort over genfund af Hættemåger ringmærket som unger i Danmark og fundet døde som a) 1.-års fugle (n = 754), b) 2.-års fugle (n = 240) og c) adulte fugle (n = 641). Prikker angiver enkelte genfund og graden af gråtone antallet af genfund per kvadrat.

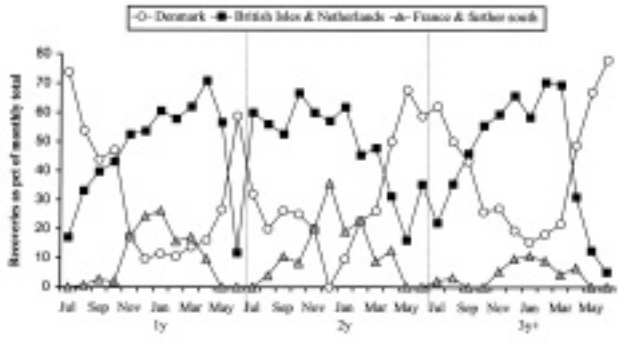

Fig. 3. The proportion of recoveries of Black-headed Gulls ringed in Denmark as chicks and recovered in the indicated areas (percent of all recoveries within the given month).
Andelen af genfund af Hættemåge ringmærket som unger i Danmark og genfundet i de angivne områder (procent af alle genfund i den pågældende måned).

Temporal and spatial distribution of recoveries. The majority of the Danish Black-headed Gulls are migratory. Recoveries came from the British Isles and western Europe with a few from southwestern Europe and northern Africa (Fig. 2a-c, Appendix 1). A cyclical pattern of annual appearance was evident from all the main geographical regions (Fig. 3).

Migration. Migratory movements were seen in all age-classes (Fig. 4). Soon after the breeding season, dispersal movements were in southwesterly directions (Table 1); this migration was initiated by the second-year birds in late June, followed by the adults in early July and the first-year birds in mid-July. The movement away from the breeding areas throughout the autumn was apparent for all age-classes, the second-year birds remaining furthest away in all months.

Median distances between ringing and recovery sites were similar for all three age-classes in winter (December-February) (Table 2, Fig. 4). The proportion remaining in Denmark increased with age (10.7% (1y), 12.3% (2y) and 17.3% (3y+)) but these differences were not significant ($\chi^2_{1y2y} < 0.005$, $\chi^2_{1y3y+} = 2.10$ and $\chi^2_{2y3y+} = 0.46$; df = 1; NS). The proportion of adults wintering in France and further south was lower than for first-year birds ($\chi^2 = 7.89$; df = 1; $p < 0.01$) and second-year birds ($\chi^2 = 6.11$; df = 1; $p < 0.02$); the proportions for first-year birds and second-year birds were similar ($\chi^2 < 0.005$; df = 1; NS).

With the origin of the birds subdivided into the geographical areas Funen (c) and the regions of Denmark west (w) and east (e) thereof, there was no significant differences in wintering area ($\chi^2_{wc} = 3.00$, $\chi^2_{we} = 2.21$ and $\chi^2_{ce} = 0.23$; df = 3; NS).

There were no significant differences in winter-

Table 1. Direction from ringing to recovery sites of Black-headed Gulls ringed as chicks in Denmark for first-year birds (1y), second-year birds (2y) and adults (3y+). r is the mean vector length and a is the direction of this vector. Asterisks denote significance levels.
Retningen fra mærkningssted til genfund af Hættemåge ringmærket som unger i Danmark for 1.-års (1y), 2.-års (2y) og adulte (3y+) fugle. r er den gennemsnitlige vektors længde og a er retningen af denne vektor. Stjerner ved vektorlængden angiver signifikansniveauet.

	Autumn *Efterår*				Spring *Forår*			
Age *Alder*	Period *Periode*	n	r	α	Period *Periode*	n	r	α
1y	21-30 June	9	0.47	199°	11-20 May	7	0.85**	242°
	1-10 July	34	0.20	271°	21-31 May	13	0.86***	234°
	11-20 July	64	0.24*	242°	1-10 June	5	0.22	312°
	1-31 July	66	0.49***	244°				
2y	11-20 June	5	0.40	195°	1-10 April	10	0.59*	258°
	21-30 June	7	0.76*	214°	11-30 April	6	0.32	226°
	1-10 July	7	0.58	248°	1-10 May	10	0.08	299°
	11-20 July	8	0.80***	235°				
3y+	21-30 June	26	0.17	152°	1-10 April	18	0.49*	232°
	1-10 July	32	0.46**	250°	11-02 April	16	0.73***	235°
	11-20 July	39	0.28*	222°	21-30 April	11	0.09	294°
	21-31 July	24	0.41*	257°				

Rayleigh test: * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Age *Alder*	n	Distance ± SE *Afstand ± SE*	U 1y	 2y
Winter *Vinter*				
1y	140	788.5 ± 47.5		
2y	57	782.0 ± 62.0	3740	
3y+	150	753.0 ± 33.9	9583	3637
Breeding period *Ynglesæson*				
1y	47	419.0 ± 42.0		
2y	48	73.0 ± 43.6	699**	
3y+	142	56.5 ± 21.1	1545***	3127

Mann-Whitney U-test: ** $p < 0.01$, *** $p < 0.001$.

Table 2. Median distances (km) from natal colony to recovery site for three age-classes of Black-headed Gulls in winter (December-February) and during the breeding period (May-June). U is the Mann-Whitney test statistic.
Medianafstand (km) fra yngle- til genfundslokalitet for tre aldersklasser af Hættemåge om vinteren (december-februar) og i yngleperioden (maj-juni).

ing area between the 1930s (a), the 1960s (b) and the 1990s (c) ($\chi^2_{ab} = 1.88$, $\chi^2_{ac} = 2.88$ and $\chi^2_{bc} = 2.95$; df = 3; NS). If shot birds were included there was a significant difference between the 1930s and the 1990s ($\chi^2_{ac} = 8.11$; df = 3; $p < 0.05$) but not between the other decades ($\chi^2_{ab} = 6.63$ and $\chi^2_{bc} = 1.91$; df = 3; NS).

Second-year birds and adults had similar spring migrations, both age-classes reaching the breeding colonies in mid-April. The first-year birds migrate later and reach the breeding colonies in early June (Fig. 4, Table 1).

In the breeding season (May, June) the median distance for the first-year birds was significantly larger than for second-year birds and adults (Table 2). The proportion of first-year birds found in Denmark in these months was lower than the proportions of second-year birds ($\chi^2 = 5.56$; df = 1; $p < 0.02$) and adults ($\chi^2 = 17.34$; df = 1; $p < 0.001$); the proportions for the latter two age-classes were similar ($\chi^2 = 0.92$; df = 1; NS).

Temporal recovery patterns. Fig. 5 compares the months of recovery for the three age-classes. Among first-year birds recoveries were most frequent immediately after fledging. Most second-year birds and adult birds were recovered during the breeding period. The monthly proportions of recoveries of second-year birds was significantly correlated to the monthly proportions of adults ($r_S = 0.66$, $p = 0.02$). The corresponding correlations between first-year birds and second-year birds ($r_S = 0.09$, $p = 0.79$) and adults ($r_S = -0.08$, $p = 0.80$) were not significant.

Mortality rates. The ratio of first-year birds to all birds recovered in each month remained high until about February when it reached an approximately constant level (Table 3). This suggests that the mortality rate equals the adult level at this time. The estimation of adult mortality rates was consequently based on recoveries from and including February in the second calendar year. That the annual survival was independent of age after the first year was supported by the approximately linear relationship between log-transformed recovery numbers and time (Fig. 6; $r^2 = 0.91$, $p < 0.0001$) and confirmed by a runs test on the same data (years 18-20 pooled: $n_1 = 7$, $n_2 = 11$, $u = 8$, $p = 0.30$).

The juvenile survival was estimated at 61.6% during the first calender year and 48.9% during the first year. On basis of the complete data (chicks ringed prior to 1983) the annual adult survival was

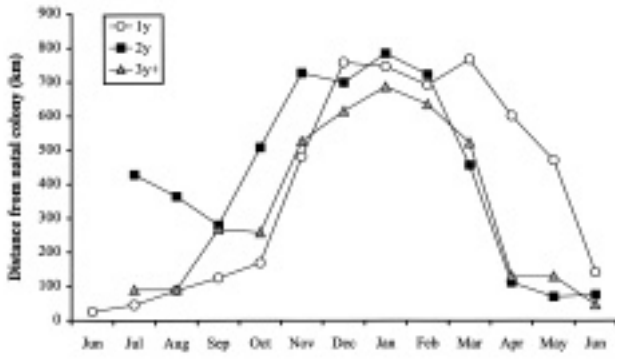

Fig. 4. Median monthly distance from natal gullery to recovery site for each age-class of Black-headed Gulls ringed in Denmark as chicks.
Månedlig medianafstand mellem ynglelokalitet og genfundssted for hver aldersklasse.

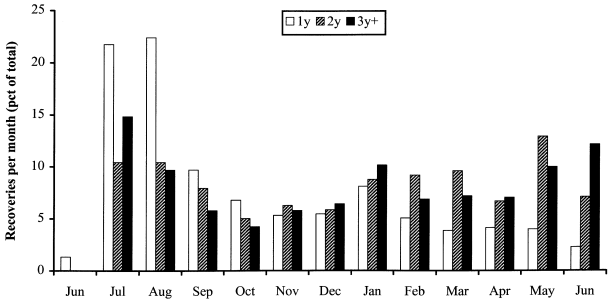

Fig. 5. Monthly distribution of recoveries for 1st-year, 2nd-year and adult Black-headed Gulls ringed as chicks in Denmark.
Månedlig fordeling af genfund af 1.-års, 2.-års og adulte Hættemåger ringmærket som unger i Danmark.

estimated at 77.4%. Recoveries from more recent cohorts yielded an estimate of 72.4%, while the estimate based on the combined material was 72.8% ± 2.1. Combining this latter estimate with that for first-year birds, and an assumed average age of first breeding at 2 years, each pair should produce 1.53 fledglings per year in order to replace adult losses (cf. Bensch & Källander 1997).

Discussion

The recovery rate has remained fairly constant over time at 2.0-2.5% except that it was much lower during the 1940s, during and after the war (Fig. 1). The recoveries from birds ringed during the 1990s are incomplete since some birds are still alive. Fewer Black-headed Gulls are shot now than earlier, whereas the number of resightings has increased.

Migration patterns. The overall distribution of the recoveries of chicks ringed in Denmark was similar to the distribution of the recoveries of Black-headed Gulls ringed in southern Sweden (cf. Bengtsson 1996). Fledglings migrated south-west soon after independence. The autumn migration was initiated by second-year birds, followed by adults and lastly first-year birds. The same pattern was apparent among migrants at Falsterbo in southern Sweden (Olsen 1992) and at Blåvand in western Denmark (Meltofte & Faldborg 1987). A second peak of adults at Blåvand may represent birds from other parts of Scandinavia and the Baltic countries.

Contrary to the suggestion of Andersen-Harild (1971) no differences in recovery area during winter for fledglings from different regions of Denmark could be demonstrated in the present analysis, and neither could a change over time in wintering area for the Danish Black-headed Gulls. Andersen-Harild (l.c.) found that such a change over time became statistically significant only if shot birds were included and therefore cautioned that the apparent change might have other causes, although this is often overlooked in works quoting his results.

Table 3. The monthly proportion of recoveries of first-year and second-year Black-headed Gulls ringed in Denmark as chicks, to older than first-year and older than second-year birds, respectively.
Den månedlige andel af genfund af 1.-års og 2.-års Hættemåger mærket som unger i Danmark, i forhold til henholdsvis ældre end 1.-års og ældre end 2.-års fugle.

Month *Måned*	1y	>1y	% in 1y	Mean *Gennemsnit*
Jul	164	120	57.7	
Aug	169	87	66.0	
Sept	73	56	56.6	59.3
Oct	51	39	56.7	
Nov	40	52	43.5	
Dec	41	55	42.7	42.6
Jan	61	86	41.5	
Feb	38	66	36.5	
Mar	29	69	29.6	
Apr	31	61	33.7	27.8
May	30	95	24.0	
Jun	17	95	15.2	
Month *Måned*	2y	>2y	% in 2y	Mean *Gennemsnit*
Jul	25	95	20.8	
Aug	25	62	28.7	27.8
Sep	19	37	33.9	
Oct	12	27	30.8	
Nov	15	37	28.8	28.4
Dec	14	41	25.5	
Jan	21	65	24.4	
Feb	22	44	33.3	30.4
Mar	23	46	33.3	
Apr	16	45	26.2	
May	31	64	32.6	25.6
Jun	17	78	17.9	

From the end of the winter the pattern of recoveries was similar for second-year birds and adults (Fig. 4). Spring migration peaked in March and April (Fig. 4), confirming observations from Blåvand (Meltofte & Faldborg 1987). In London the main departure of wintering Black-headed Gulls occurred in mid-March (Christmas et al. 1986).

The recoveries of first-year birds were made further from their natal colony than older age classes between January and the following December (where they have become second-year birds) (Fig. 4). During spring they lagged two months behind the older birds. Not until June were first-years recovered close to the natal colony, and both in May and July the median distance between recovery and colony was more than 400 km, showing that few Black-headed Gulls breed in their second year.

Mortality. The high proportion of first-year birds recovered in the first few months after independence reflects a high mortality during this period, as is the case for most other birds (Anderson et al. 1985). The high recovery rate observed for adults during the breeding season probably reflects a high probability that dead birds in a colony will be found, particularly if ringing activities are going on. There was no excess mortality during winter, possibly because Black-headed Gulls leave areas with severe winter conditions (van Dijk 1993).

The estimated survival during the gulls' first year of life (49%) was higher than found in other studies, but the difference is rather small and probably not significant (e.g. 44%, Glutz & Bauer 1982). The annual adult survival (73%) was within the range of other studies (Glutz & Bauer 1982).

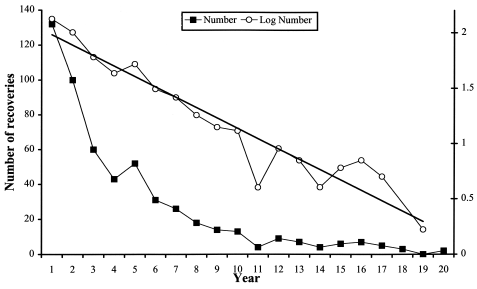

Fig. 6. Recoveries of Black-headed Gulls ringed as chicks prior to 1983, excluding recoveries during the first year of life.
Genfund af Hættemåger ringmærket som unger før 1983, med undtagelse af genfund fra første leveår.

Whether the rough estimate of 1.53 fledglings per pair needed to maintain a stable population has any relevance in connection with the recent population decline of the species (Heldbjerg 2001) is unclear, owing to the character of the estimate and because nothing has been published about young production in Danish Black-headed Gulls. On nearby Swedish localities, likewise with declining numbers (Källander 1996), the reproductive output was found to be insufficient to maintain the population (Bensch 1992, Bensch et al. 1996).

Acknowledgments

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Resumé

Træk og overlevelse af Hættemåger *Larus ridibundus* **ringmærket som unger i Danmark**

I årene 1931-1998 er der ringmærket 133 883 unger af danske Hættemåger i Zoologisk Museums regi (Fig. 1). I denne analyse er genfund med unøjagtige genfundsdata, genfund nærmere end 10 km fra mærkningslokaliteten samt unger fra Færøerne udeladt. Endvidere er skudte fugle (i aftagende antal gennem perioden) og aflæste fugle (stigende antal) ligeledes udeladt. Herefter indgår der i alt 1635 genmeldinger. Første års (1y), andet års (2y) og adulte fugle (3y+) er, med 1. juli som skæringsdato, behandlet separat. Fordelingen af genfund viser, at de danske ynglefugle hovedsagelig trækker til de Britiske Øer og Vesteuropa, men nogle når så langt som til den Iberiske Halvø og Nordafrika (Fig. 2, Appendix 1). Andetårsfuglene trækker mod sydvest i slutningen af juni, de adulte følger i starten af juli, og førsteårsfuglene i midten af juli (Tabel 1). I hele sensommer- og efterårsperioden befinder andetårsfuglene sig længere fra ynglelokaliteten end de to andre aldersklasser (Fig. 4). Den tilsvarende afstand om vinteren er ens for alle aldersklasser (Tabel 2), men en større andel af 1.-års og 2.-års fuglene end de adulte overvintrer i eller syd for Frankrig (Fig. 3). I modsætning til den tendens, Andersen-Harild (1971) fandt, ses der i dette materiale ingen forskel i overvintringsområde mellem 1930erne, 1960erne og 1990erne, og ej heller mellem ynglefuglene fra Jylland, Fyn og øerne øst herfor. Om foråret trækker 2.-års og adulte fugle mod yngleområdet på samme tid og afslutter trækket i midten af april, hvorimod 1.-års fuglene først afslutter trækket i slutningen af juni (Fig. 4, Tabel 1). Afstanden til genfundene i ynglesæsonen er

signifikant større for 1.-års fugle end for 2.-års og adulte fugle (Tabel 2), hvilket stemmer overens med, at hovedparten af Hættemågerne yngler første gang som toårige.

Førsteårsfuglene genfindes i størst tal i månederne umiddelbart efter at de er blevet flyvefærdige, hvilket må tilskrives høj dødelighed pga. manglende erfaring (Fig. 5). For 2.-års og adulte fugle sker genfundene hovedsagelig i yngleperioden. Den juvenile overlevelse i det første kalenderår er beregnet til 61,6% og i det første leveår til 48,9%; den antager adult størrelse fra februar i andet kalenderår (Tabel 3), og siden sker der ingen påviselige ændringer i den. Den årlige adulte overlevelse er beregnet til 72,8%. På baggrund af disse overlevelsesrater er den nødvendige produktion af flyvefærdige unger pr par beregnet til 1,53, hvis den nuværende bestandsstørrelse skal opretholdes. Desværre er danske Hættemågers ungeproduktionen aldrig blevet undersøgt, men i det sydlige Sverige ser ungeproduktionen ud til at være betydeligt mindre end angivne 1,53 pr par. En svigtende ungeproduktion kan derfor være en del af forklaringen på den nuværende tilbagegang i den danske bestand.

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Appendix 1. Recoveries of Black-headed Gulls *Larus ridibundus* ringed in Denmark as chicks.
Genfund af Hættemåge Larus ridibundus *ringmærket som unger i Danmark.*

	1st year after ringing													2nd year after ringing											3rd year after ringing and later											
	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Jan	Feb	Mar	Apr	May	Jun
Norway		1	1						1																												
Sweden		5	1	1									1		1									2	1	3								1	2	3	2
Finland																										1		1								1	
Denmark	9	121	91	32	24	7	4	7	4	4	5	8	10	8	5	5	3	3		2	5	6	8	21	10	59	31	16	7	10	8	10	8	10	22	43	61
Germany		9	18	8	4	4	4		1		1	5	4	2	4	2				1		2		2		8	7	3	4	2		4	1	1	3	7	11
Netherlands		21	29	15	11	12	9	14	10	5	9	8		4	4	3	4	4	2	4	4	5		1	3	11	10	4	6	3	10	8	5	10	3	3	
Belgium			1	1		1	1	1	4	1									1	1	2	2	1	1		1			1		2	5			1		
France			1	1	1	6	9	9	4	2	1				1	2		3	4	3	4	1	2			1	2			2	3	6	3	2	3	2	
Scotland											3		1						1								2								1	1	
Ireland				1		1	1	2		1																1	1			1		2					1
Wales			3		1		1					1			1			1		1			1			1	2				2	1	1	2			
England	1	7	24	13	10	8	11	21	12	12	10	8	1	11	9	7	4	4	5	8	6	6	4	4	3	8	7	13	9	18	15	27	25	20	10	4	3
Switzerland										1																				1		1					
Spain						1	1	6	1	3	1						1		1	1						1					1	1					
Portugal				1				1													1	1										1					
Morocco									1		1																										
Sum	10	164	169	73	51	40	41	61	38	29	31	30	17	25	25	19	12	15	14	21	22	23	16	31	17	95	62	37	27	37	41	65	44	46	45	64	78