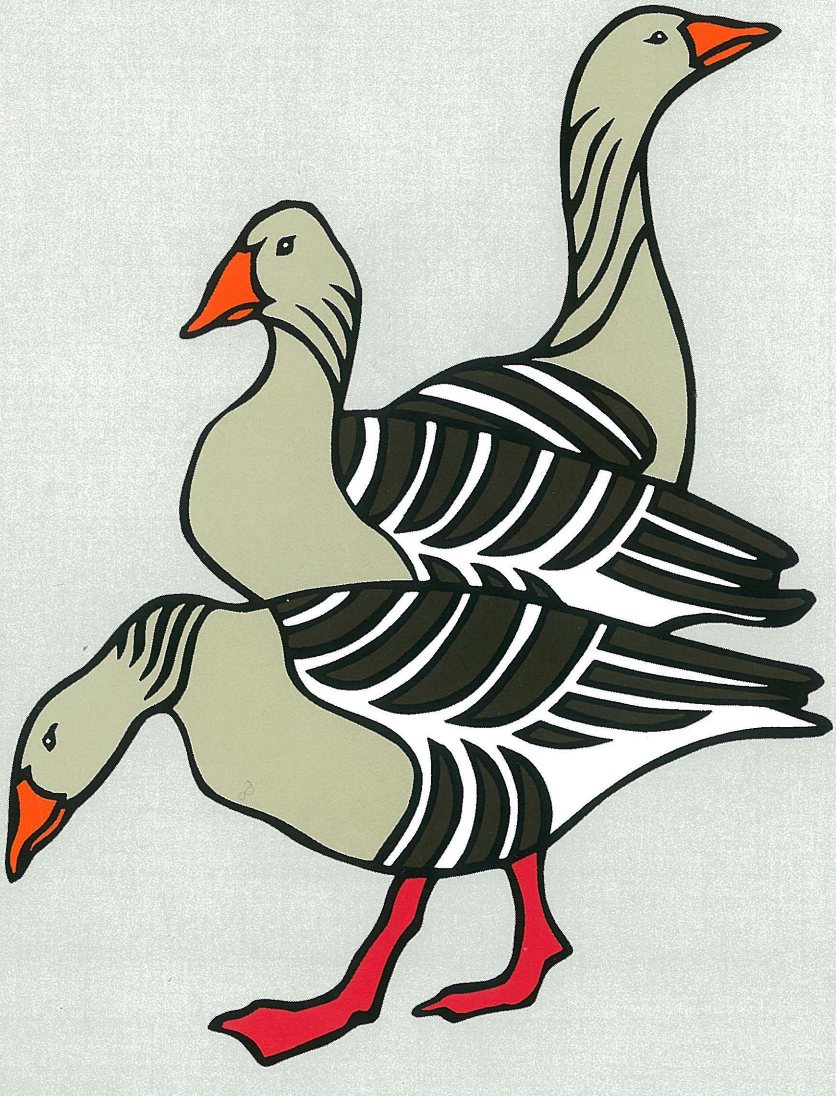
The Greylag Geese of Utterslev Mose

KAJ KAMPP AND NIELS OTTO PREUSS



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Individually marked Greylag Geese *Anser anser* were studied during 1959-1994 in Utterslev Mose (UM), a park and lake area in Copenhagen, Denmark. During the study period the population increased from less than 100 to more than 200 pairs, with two temporary set-backs in the early 1970s and the early 1980s, respectively – the first caused by local factors in UM, the second by problems with the water regimen in the most important wintering area, Doñana in Spain. The breeders returned to UM in February and March, hatching their clutches in late April and May. A total of 1165 of the marked geese were recovered dead, a great majority from the four countries Denmark, Netherlands, France and Spain; 86% of them were shot.

Survival of goslings from ringing to the following spring was estimated from the number of returned females, since almost all surviving females will settle and breed in their natal area. Although varying considerably between years, this first-winter survival increased through the study period, from about 0.50 to 0.64. Return rates of male goslings decreased and were only about half as high as those of females towards the end of the study; many males emigrate and settle outside the natal area, however, and males probably survived about as well as females. Survival of older birds was likewise estimated from return rates, since very few birds – females and males alike – appear to leave UM when first established here; the overall mean for birds at least five years old was 0.70 for females, 0.77 for males, again with much variation and with an increasing trend. Females ringed as adults survived significantly better than females ringed as young but at least five years old, showing that in bird-ringing analyses, birds ringed as adults are not always equivalent to 'old' birds ringed as young. Shooting appeared to be an important mortality factor for both young and old birds, and the decreasing mortality rates during the study period coincided with a decreasing level of shooting.

On average, females first paired when 1.9 years old. Corresponding ages for first breeding attempt, first successful hatching, and first successful breeding, were 3.3, 4.2 and 4.5 years, respectively. Males started at similar ages. Breeding propensity increased until the birds reached an age of about six years, where 70-80% bred in any given year. Nest success of old breeders was roughly 0.7, but lower in younger birds. Brood success cannot be calculated owing to widespread occurrence of brood amalgamation in UM, but gosling survival from shortly after hatching to ringing after about six weeks was high, about 0.9. Initial brood size varied without any time trend, with an overall mean of about 5 goslings; it appeared to increase with the age of the female parent until at least five years. Breeding propensity and success were adversely affected in newly formed pairs after the death of a former mate, or after a 'divorce'.

The post-fledging survival of goslings was weakly, but significantly connected to parent age; it increased with the age of the mother, whereas a peak survival of fledglings having middle-aged fathers (6-10 years) was suggested. Fledglings from early broods also appeared to survive better than fledglings from late broods, but this may essentially have been an effect of parent age, since older birds bred earlier. The body mass of goslings at ringing also affected their apparent survival: heavy females were more likely to return than light females, probably because they survived better. Curiously, however, heavy males were less likely to return than lighter males, presumably because they were more liable to emigrate. Although suggested in some other goose studies, no relationship between brood size and survival could be found. Finally, post-fledging survival was affected by the death of one or both parents before the following spring, as would be expected in a species where parents and offspring stay together during this period. The loss of the father appeared to have the greatest effect. Nevertheless, some goslings did survive, even after losing both parents in the early autumn.

The lifetime reproductive success (LRS) and its variation could be estimated for females born in 1981 or before. Of an estimated 794 fledged females, 241 settled in UM and reached an age of two years, so had a chance to breed. Together with a few other females that produced at least some of their offspring elsewhere, these females produced an estimated 1620 fledglings. Of the 241 regular UM females, 125 produced at least one brood, the most productive hatching 71 goslings; 17% of the 125 females produced 50% of the goslings. Longevity was the most obvious factor influencing LRS, although the success of females attaining similar ages varied considerably. An early breeding start did not seem to be important, and neither did the birth year of the female, except that unusually few females from the late sixties produced any young.

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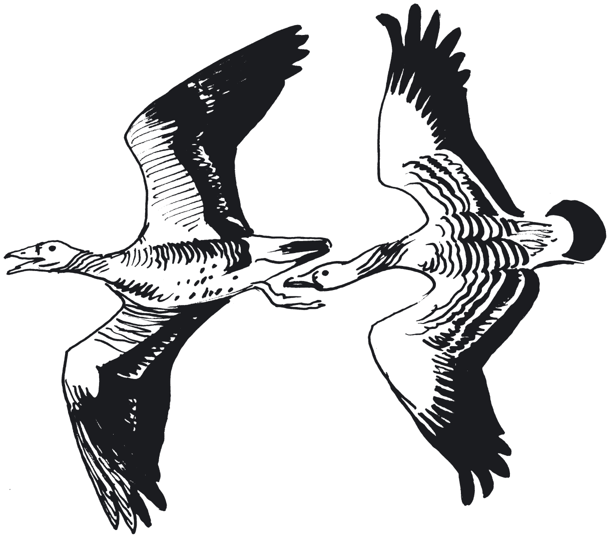
The Greylag Geese of Utterslev Mose

A long-term population study of wild geese in an urban setting

Kaj Kampp and Niels Otto Preuss



Med et dansk resumé: Grågæssene i Utterslev Mose

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Contents

Introduction

Population studies of birds have been undertaken for a range of purposes (cf. for example Perrins et al. (1991)). Many such studies have addressed questions based on individual recognition, and some have been of long duration in order to, for example, ascertain sufficient statistical power when measuring time trends, or to answer questions about longevity, lifetime reproduction, or intergenerational issues. Long-time studies were not always planned and designed from the outset – on the contrary, "they tend to evolve as opportunities and chance permit, and as the commitment of the investigators persists" (editorial introduction to Dunnet 1991).

One example is the study of Greylag Geese *Anser anser* at Utterslev Mose, Copenhagen. It was initiated in 1959 by Erik Petersen – who sadly died in 1961 – and the second author, who was then director of the bird ringing centre at the Zoological Museum, University of Copenhagen, and ended when NOP retired in 1995. Inspired by projects like the Dutch Great Tit *Parus major* study (Kluijver 1951) and the pioneer work on Yellow-eyed Penguins *Megadyptes antipodes* by Richdale (1957), the study mainly aimed at measuring components of demography and population dynamics, although the purpose was not very precisely defined; to some extent, it was a question of taking the fortuitous and unique opportunity of having a breeding population of wild geese within easy reach at an urban park and lake area in Copenhagen. That the birds gradually became accustomed to the many people frequenting the park, and grew very tame, was an extra bonus.

Today, wild geese are among the most intensively studied birds. They are important quarry species, and for an increasingly urbanised public they have great recreational value. On the other side of the coin, they may damage crops. And for ecologists geese have many characteristics that make them ideal study species. It is not surprising, therefore, that although the Utterslev Mose project apparently was the first long-term goose study to be initiated, it was not the only one. Among the more widely publicised studies are those concerning, respectively, the Lesser Snow Goose *Anser c. caerulescens* with the focus on the breeding colony of La Pérouse Bay at the shores of Hudson Bay (Cooke et al. 1995), and the Svalbard population of Barnacle Geese *Branta leucopsis* studied each year on the wintering grounds and periodically in the breeding area and at staging sites during migration (many papers by M. Owen, J.M. Black and others, many cited below); both studies were initiated around 1970. A Greylag Goose study was started in south Sweden in 1984, using neck-collared birds so that the same individuals could be followed throughout their annual cycle (Nilsson 1998).

Unfortunately, very little has been published until now from the Utterslev Mose project and its results (Petersen 1960, Petersen & Preuss 1962, Preuss 1960, 1964), and after the retirement of NOP there was a real risk that all the effort invested in the study would be wasted, and the data forgotten. It was therefore very fortunate that Aage V. Jensen Charity Foundation in 2002 granted the first author financial support to analyse the data, resulting in the present publication.

It was considered most appropriate to present the data extensively, examining as many of the fitness components (*sensu* Cooke et al. 1995) as possible, and in so doing expose the strengths and weaknesses of the data. This means that there is still room for more in-depth analyses of specific topics. Although there is a good deal of numbers and statistics to be found in the present publication, the potential of the dataset is far from exhausted, and interested investigators may still find a lot of valuable information there. Copies of the database have now been deposited at the Ringing Centre, Zoological Museum, University of Copenhagen, as well as the Department of Arctic Environment under the National Environmental Research Institute.

Photo: Knud Falk.

The Greylag Goose in Denmark

Greylag Geese breeding in Denmark belong to the west Baltic population, the breeding range of which besides Denmark includes Sweden, north Germany, north Netherlands, west Finland, northwest Poland, and south Bohemia (Kampe-Persson 2002). A large majority of these geese winter in Spain and the Netherlands, although a small (but increasing) proportion of the Danish breeders stay in Denmark over winter (Grell 1998).

The Danish breeders return in February-March while yearlings arrive some weeks later. Laying takes place in late March – early April, with peak hatching four weeks later. The goslings attain flight at an age of about 60 days (56-69 days, Kampe-Persson 2002). Non-breeders begin to congregate at moulting sites during May, whereas successful breeders moult at the breeding sites. After completing moult the geese gradually move to autumn staging sites before continuing to the winter grounds. Formerly, a large majority of the west Baltic population spent the winter months in the Guadalquivir Marismas in SW Spain, but since the 1980s other sites, in the northern part of the country, have become increasingly important, and especially since about 1990 the number of birds staying in the Netherlands has grown dramatically (Nilsson et al. 1999). However, the Marismas is still extremely important for wintering Greylag Geese. The distribution of the Danish geese on Dutch and Spanish wintering grounds cannot be quantified with any precision since, in the absence of neck-collaring studies, the only source of information is recoveries of ringed birds (mostly by shooting), and hunting pressure as well as the probability that found rings are reported will certainly differ greatly between areas.

The populations migrating along the East Atlantic Flyway have experienced a marked increase during recent decades; mid-winter estimates thus comprised about 30 000 birds in 1967/68, but almost 200 000 in 1994/95 (Madsen 1987, Nilsson et al. 1999). The west Baltic population numbered 250 000-325 000 birds in the early 2000s (Kampe-Persson 2002). Estimates of breeding numbers in Denmark during the period of the present study have grown from 750-1000 pairs in 1960 (Preuss 1983) and 2850-3000 pairs in the mid 1970s (Fog et al. 1984) to 3200-3500 pairs in the early 1990s (Jørgensen et al. 1994).

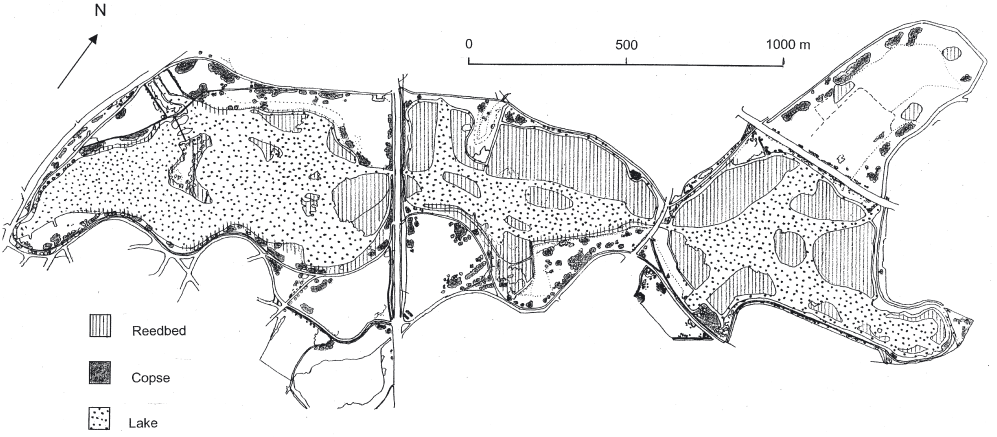


Fig. 1. Map of Utterslev Mose in Copenhagen. Field map used during the study period, 1959-1994.
Kort over Utterslev Mose.

Study area

When Utterslev Mose (Fig. 1) was made a park in 1939-1943, a swampy, overgrown area was transformed into a series of lakes with adjoining lawns and smaller patches of scrub and trees (Kaulberg 1947, Fjeldså 1973, Fjeldså & Boertmann 1980, Jensen 1998, Københavns Kommune pamphlet 2001). The total area, situated between Copenhagen and Gladsakse municipalities (55°43' N, 12°31' E), is about 200 ha, half of which is lake and islands. Today, the park is completely surrounded by built-up areas, and two roads divide the area into three parts (west, mid, east). The depth of the water is 0.5-1.5 m, in the mid section up to 2 m, and while lawns extend right to the water's edge at some places much of the shore is fringed by reeds, with more extensive reedbeds occurring in the east and mid sections. The reedbeds are separated from the shore by canals, and there is no public access to the lake surface or islands (boats are not allowed). Foxes *Vulpes vulpes* do occur, but have very rarely been able to access and kill incubating females, and even predation on goslings appears to be minor.

During the 1960s the water quality deteriorated owing to admission of raw or poorly processed sewage water, and to an insufficient water supply leading to falling water levels. Beginning in 1970, the municipality of Copenhagen has made great efforts to improve the situation, by limiting the sewage discharge and increasing the water level and flow through the lakes; at the same time the islands were protected with anti-erosion stockades. In 1998 a water treatment plant began to remove plant nutrients from the water, and although the three lakes are still strongly eutrophic, the water quality of Utterslev Mose is gradually improving.

Utterslev Mose (occasionally abbreviated UM in the following) is, or has been, an important breeding site for several species of waterbirds (Fjeldså & Boertmann 1980): Little Grebe *Tachybaptus ruficollis*, Black-necked Grebe *Podiceps nigricollis* (now disappeared), Pochard *Aythya ferina*, Tufted Duck *A. fuligula*, and Coot *Fulica atra*. Around 1970 the colony of Black-headed Gull *Larus ridibundus* was one of the largest in the world, comprising c. 20 000 pairs, but numbers have since decreased to about 3000 in the late 1990s (Heldbjerg 2001).

A few pairs of Greylag Geese have bred at Utterslev Mose at least since 1914 (Kaulberg 1947, Fjeldså & Boertmann 1980). Around 1950 numbers started to increase, in parallel to numbers in the rest of the country, and by the early 1960s – at the beginning of the present study – there were more than 50 pairs. Numbers have since fluctuated, but the last decade of the study has seen an almost uninterrupted increase, to more than 200 pairs in 1994 (see below). The geese breed on the reedy islands and in the reedbeds but graze on the lawns, and as long as they reside in the park they exhibit an extraordinary lack of fear of humans, permitting approach down to a few meters and sometimes even accepting food (bread) directly from the hand. This has not always been the case, however, and in the 1960s, during the first years of the study, the geese were much more shy.

The geese usually begin to arrive in February or early March, although smaller numbers may forgo migration and stay over winter, at least in mild winters. The adults arrive first, while yearlings on average turn up a few weeks later, indicating that they often separate from their parents before arrival at the breeding grounds. In addition to the local geese, some birds from other breeding localities may stage at the site during the first days after arrival, or may appear – and sometimes moult – there after the breeding season.

Material and methods

Fieldwork

Since 1959, the majority of the goslings at Utterslev Mose have been captured in pens and ringed when 4-6 weeks old. In addition to a metal ring from the Danish ringing system, based at the Zoological Museum of the University of Copenhagen, the goslings were supplied with three colour rings of plastic on the other leg, permitting individual recognition at subsequent sightings in the same and later years. Nine colours were used (white, black, grey, dark blue, light blue, dark green, light green, yellow, red), permitting $2 \cdot 9^3 = 1458$ combinations. The total number ringed exceeded by far this number, so it became necessary to re-use combinations from birds known to be dead, or not seen for a long time. In practice, the risk of mis-identification following from this procedure was negligible, because re-use of combinations first started well into the study period, when the geese had grown very tame, and because the metal rings were easy to read even from a distance, bearing two copies of the number in large types.

There has been no indication during the study that any of the geese had lost its metal ring. The colour rings were glued together, and only rarely did a bird loose some or all of them.

Photo: S. Springborg.

Ringing geese in Utterslev Mose, 1987. A flock of flightless goslings and adults is surrounded and driven towards a pen.
Ringmærkning af gæs i Utterslev Mose, 1987 – den indledende fase.

With exception of the first years (1959-1963, 1965) the goslings were sexed by cloacal examination, and from 1968 most goslings were weighed to the nearest 10 g. Usually, a few adults have also been captured during the drives, so a varying number of adults have likewise been ringed with metal and colour rings each year. Often, but not always, these adults were parents of some of the captured broods (or, at least, were guiding them). Numbers ringed during 1959-1994 are shown in Table 1.

Numbered neck-collars offer better opportunities of obtaining sightings from biologists not involved in the study, and even from the general public. However, the option of using neck-collars was precluded by the fact that the study area was an urban park within a major city. The convenience of having a large population of unusually tame geese at hand at an easily accessible site therefore also limited the acquisition of sighting data to the study area itself. Each year, NOP or an assistant visited Utterslev Mose for 1-3 hours on most days from the arrival of the geese to well into July. During these visits, all observations of ringed geese were recorded on pre-printed forms according to a fixed protocol. Apart from the colour code (and occasionally the number of the metal ring), the items noted were the apparent sex of the bird, whether it was accompanied by a mate, whether it was guarding goslings and if so their number, and where within the study area it was seen.

This procedure typically yielded 100-200 observations in any year of a bird regularly present throughout the breeding season. Some non-breeders or visiting birds were recorded less frequently, and records of those occurring very rarely could not always be distinguished with absolute certainty from the occasional inevitable errors. Suspicious cases were judged by comparing with previous observations (if any) of the colour combination in question, and if doubt still remained the record was deleted from the database.

Observations were kept as unintrusive as possible. No geese were disturbed or handled except during ringing. Neither was any attempt made to identify the owners of nests found during monitoring work in the park, which might have led to investigator-induced nest desertion (Witkowski 1983). While the procedure thus ensured that the study objects behaved as 'naturally' as possible, it also precluded the acquisition of some valuable information. Also, some doubt remained about the breeding status of a minor proportion of the birds. The criteria used to determine if a pair laid were the absence of the female (but not the male) in the usual incubation period and, if she happened to be seen during her rare feeding bouts, the very characteristic behaviour during such occasions; in addition, after a couple of weeks the tarsus of an incubating female becomes distinctly paler. Successful hatching was indicated by the appearance of the goslings when they started to graze on the lawns after a few days. The laying of a pair losing or deserting a clutch early in the incubation period, hence, could easily go undetected, as would the hatching if the goslings survived or remained with their parents for a very short period only.

Sex determination of goslings

The determination of sex in goslings and other anatid young by cloacal examination is not perfect, and the occasional mistake will happen. From subsequent behavioural observations of breeding Mute Swans *Cygnus olor*, Brown & Brown (2002) found that 11% had been incorrectly sexed when ringed as young, although sexing of cygnets may be done reliably if other characters are also considered (weight and other biometrics; P. Andersen-Harild pers. comm.). It can be a time-consuming procedure, however, and time is generally constrained when a batch of penned goslings await processing. In case of the Utterslev Mose goslings, therefore, some mis-sexing was to be expected. Furthermore, when dealing with geese, and keeping the focus at one breeding locality, great care has to be taken in order to define 'erroneously determined sex' in a meaningful way. Also, the consequences of mis-sexing for the subsequent analysis may be grave.

The main reason for these problems is the female-biased return rates to the natal site. This means that a mis-sexed 'male' (i.e., a female) is much more likely to return than a correctly sexed

Table 1. Annual numbers of Greylag Geese ringed as adults or goslings at Utterslev Mose, 1959-1994. Sex as determined at ringing: F female, M male, F? probable female, M? probable male, unkn unknown (not sexed).
Antallet af Grågæs ringmærket i Utterslev Mose hvert år i undersøgelsesperioden. Kønnet er angivet som det blev bestemt ved mærkningen: F hun, M han, unkn ukendt.

	Adults						Goslings						Total
	F	M	F?	M?	unkn	Total	F	M	F?	M?	unkn	Total	
1959					3	3					24	24	27
1960		1			13	14					70	70	84
1961					7	7					53	53	60
1962					20	20					80	80	100
1963		1			8	9					38	38	47
1964	8	6				14	28	33	2	2	27	92	106
1965	1	1				2					54	54	56
1966	4	7				11	18	24		1	2	45	56
1967	3	2	1	1	17	24	83	79	4			166	190
1968	4	6				10	37	55	2	2	2	98	108
1969	1	7				8	38	31		1	4	74	82
1970		1			1	2			1		2	3	5
1971	3	1				4	8	3				11	15
1972	5	1				6	21	27	2	1	5	56	62
1973		3				3	24	25	3			52	55
1974	1	1				2	16	14	1			31	33
1975	15	32				47	45	48	1		1	95	142
1976	11	9				20	55	72		3	3	133	153
1977	8	6				14	61	47	1	3		112	126
1978	4	12			1	17	97	96	7	6		206	223
1979	1	1				2	16	24		1	1	42	44
1980	1	3				4	33	22				55	59
1981	1	2				3	12	12				24	27
1982	4	8				12	61	61	1	3		126	138
1983	1	7				8	57	38	1			96	104
1984	9	7				16	46	60	1		1	108	124
1985	2	11			1	14	68	66				134	148
1986	6	11				17	44	52		1		97	114
1987	12	20				32	55	65	1	2		123	155
1988	5	14				19	87	90				177	196
1989	20	31				51	119	141	2	2	2	266	317
1990	2	11				13	99	82		2	3	186	199
1991	13	12				25	52	60			5	117	142
1992	9	13			1	23	90	95	1	1	3	190	213
1993	6	7				13	76	92			1	169	182
1994	3	11				14	115	107			1	223	237
Total	163	266	1	1	72	503	1561	1621	31	31	382	3626	4129

(true) male, while the opposite applies to females. Also, the subsequent sexing of full-grown geese after they returned one or more years later was based on appearance and behaviour, and was done much more reliably when the geese were paired, and especially when they bred. The implication is that sex-specific survival and emigration rate during the first year of life cannot be assessed with the precision that would be possible if the true sex of all goslings were known. In addition, if survival of both sexes during the subsequent years is estimated on basis of true sex (instead of the sex score at ringing), the results for the first few years of life are biased upwards, because the sample of 'truly' sexed geese is biased in favour of the longer-lived birds.

Ringing geese in Utterslev Mose, 1987. In the pen the birds are placed in bags to keep them calm until they can be processed – ringed, measured, weighed, and sexed by cloacal inspection. Photo: S. Springborg.
Ringmærkning af gæs i Utterslev Mose, 1987. Efter at være gennet ind i en indhegning anbringes fuglene i sække, så de forholder sig roligt, indtil det bliver deres tur til at få et sæt ringe og blive målt, vejet og kønsbestemt.

A further complication in the Utterslev Mose data is that not all gosling were sexed (correctly or incorrectly). The majority of the unsexed goslings are from the early years, 1959-1963 and 1965, where sex-determination was not attempted, but a few were left unsexed even in other years (Table 1). A fair number of these birds subsequently settled and bred at Utterslev Mose, so simply to disregard unsexed goslings would imply a significant reduction of the dataset.

The method used to estimate probabilities of mis-sexing is presented in Appendix 1.

Organising the data

During the 1980s the data accumulated since 1959 were stored electronically in a database, with subsequent annual updates. Apart from raw data the main part consisted of two files, here called *GsRing* and *GsArkiv*.

GsRing held the ringing information, with one entry (record) for each ring number used at Utterslev Mose during the study. Also, some UM geese bred in the nearby Kagsmosen during the years 1969-1975, and these birds, and their offspring, were included as well. Apart from the ring number and the colour code, each record contained information on the date and year, the sex of the bird as recorded at the ringing occasion (female, probable female, male, probable male, or unknown), the age of the bird (gosling, adult (= at least one year old)), the identity of the female and male parent, if known (for most goslings since 1968 and a few even in 1965-1967), the former ring number if the bird had already been ringed and was given a new ring at the occasion (adults only), the weight of the bird (goslings, since 1968), and for goslings the date when first seen, usually two-four days after hatching, and hence its age (in days) at ringing.

GsArkiv contained annual summaries of the resighting data, with one entry (record) for each bird each year during its (known) life span. Birds ringed as adults were included from the year they were ringed, birds ringed as goslings from one year after ringing, provided that they were known to have survived until the spring. Each bird had a unique ID code (the number of its metal ring, or the first ring if the bird had been re-ringed). Apart from the ID code, the year, and some redundant information copied from *GsRing*, the records contained fields for the sex of the bird as determined from observations during the year in question, the ID of its mate (if any), dates for the first sighting of the bird, its mate, and its offspring (if any), the size of its brood (number of goslings) when first seen and when ringed, and codes for the birds' status and the extent to which it adopted goslings, in addition to a 'remarks' field containing further information, if necessary. Status codes were allocated for 1) not seen during the season in question, 2) seen as unpaired, 3) paired without breeding, 4) laying (or female partner laying) without hatching young, 5) hatching young but losing them before ringing, 6) hatching young and rearing them at least to ringing age, and 7) unknown because of too few sightings. Adoption codes were given to classify parents into four groups according to the number of goslings they adopted in a given season (see p. 36f).

In connection with the present analysis the files were transformed to spreadsheet format (Excel), modified and corrected. One modification was the addition of a 'final' sex assignment based on conclusions drawn each year the bird was seen. Annual sex assignments might differ for a few of the geese, but a firm conclusion could usually be reached by considering the full history of the bird and/or its mate(s). For a number of birds, however, the question had to be left open. These cases all concerned birds failing to produce young in any year, and staying at Utterslev Mose for a few years only.

No database is likely to be free of errors, but at least the most obvious – and probably (almost) all that matter – in the present one have been corrected. These include common errors during data entry, such as duplicating input or the omission of an entry (so that the field value from the previous record is carried over). It also turned out that a number of birds had been left out entirely from the database, but fortunately their records were available on paper. Other errors probably reflect transcription errors at some stage; they include (mostly small) differences between the arrival date of a bird and the mate-arrival date of the bird's mate, differences in gosling numbers given for a bird and its mate, etc. In such cases the base was corrected so that the inconsistency – internally in the database and between the database and the handwritten material – was removed. Finally, sometimes a mate ID in the record for a bird was not reciprocated in the alleged mate's record. Such inconsistencies invariably turned out to apply to cases where one of the birds had acquired a new mate after losing or divorcing another earlier in the same season; such a situation could not be dealt with in an fully satisfactory way within the given framework, but by letting the mate ID refer to the last mate only – the mate with which a brood (if any) was shared – and deleting the mate ID from the record of lost/abandoned mates, the consistency at least was restored.

The original *GsRing* contained ringing data for a few geese ringed at other localities that had later immigrated to Utterslev Mose. In the present context, and except for the above-mentioned birds breeding in Kagsmosen during 1969-1975, such birds have been treated as if they were ringed as adults at Utterslev Mose during the year they were first recorded there.

The project data as described were supplemented by an extract from the recovery files of the Danish Ringing Centre at the Zoological Museum, Copenhagen, covering all birds ringed at Utterslev Mose within the project period 1959-1994 and recovered before 2003. Recovery information for goslings recovered dead during their first year of life (hence not included in *GsArkiv*) was placed in a separate file (*Genm1y*), while data for all other birds recovered dead were added to *GsArkiv*. For several suspicious recoveries, particularly of females recovered one or more years after last being seen at Utterslev Mose, the original letter reporting the recovery was examined, in a few cases disclosing an error in the recovery file.

A file containing goose observations (mainly by Christine Pedersen) from Utterslev Mose during 1995-1998, after the termination of this study, was supplied by K. Pedersen of the Zoological Museum. These data have only been used to a limited extent, mostly to ascertain whether a few particularly 'interesting' birds were still alive after 1994, i.e., whether their full history was or was not included in *GsArkiv*.

Analyses and terminology

Most analyses in this work are more or less self-explanatory, and where supplementary information is needed, it is given in context with the topic in question. However, some terms are used in a specific meaning that may not be obvious, and in order to make them easy to find, the definitions are all placed here.

apparent survival – used synonymously with return rate.
arrival, date of (in spring) – day of first sighting in a given year.
age of gosling – number of days since first seen at brood-rearing area a few days after (true) hatching.
brood – assembly of goslings reared by a pair, including adopted goslings (if any).
fledging success – proportion of broods from which at least one gosling fledges (in practice, survives to ringing age).
hatching date of gosling – day when first seen at brood-rearing area a few days after (true) hatching.
nesting success – proportion of nests that hatch at least one gosling; in practice, proportion of laying pairs later seen with goslings.
post-fledging survival – used synonymously with first-year survival (see *survival*).
regular – used to characterize geese that were recorded at UM each year they were known to be alive, or at least were never missing for more than one year in succession. Stays in contrast to immigrant, emigrant, temporary emigrant, and visitor.
return rate – proportion of birds included in the database for year n that were also included for year n+1, or for first-years, the proportion of those ringed in year n that were included for year n+1.
survival (annual) – for yearlings and older birds in practice between end of UM season (July) and spring arrival in the following season, the few deaths occurring between arrival and July being treated as happening in the next period. For first-years between July and end of March.
weight residual of gosling – difference between weight at ringing and weight predicted for the same age when regressing weight on age for all goslings of the same sex.

Statistics

Statistical methods used throughout the present analysis are standard. As a general rule, the G-test is preferred to the χ^2, among other reasons because of the additive property of the G (partitioning). While means are generally compared using the usual t-test, there are a number of occasions where unequal variances are indicated. In most such cases, means are compared using the t' of Sokal & Rohlf (1981). Degrees of freedom are usually given as an index on the test variable.

In the text, the term 'statistically significant' is often used rather loosely where significance levels are less than 0.05. There is nothing magical about this limit, however, so the actual significance levels given throughout deserve more attention than any verbal label that may be attached.

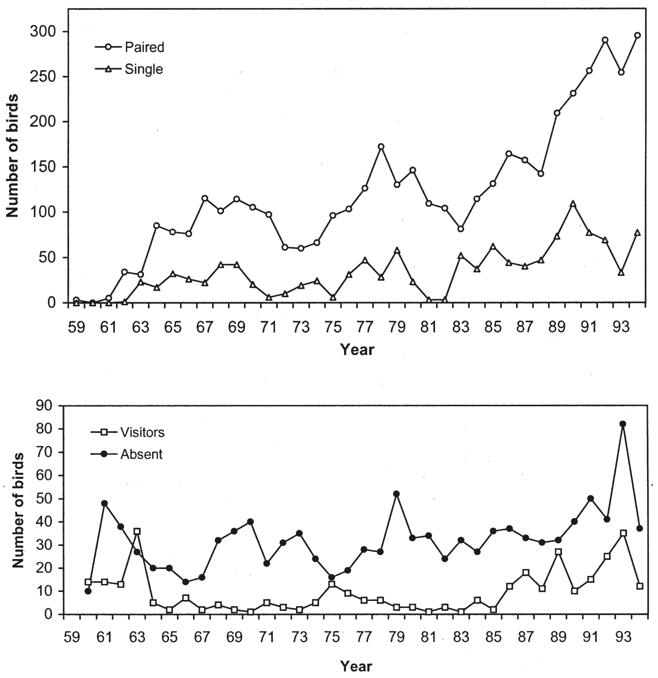


Fig. 2. Number of locally ringed Greylag Geese recorded in Utterslev Mose during the study. Birds ringed as adults are included from the year of ringing, birds ringed as goslings from the first year after ringing. Top: paired and unpaired birds regularly recorded during the season. Bottom: visiting birds not regularly seen during the season; and birds known to be alive but absent in the given year.
Antallet af UM-mærkede Grågæs, der hvert år blev set i mosen. I øverste graf er vist antallet af udparrede (cirkler) og af uparrede fugle (trekanter) set regelmæssigt, i nederste graf antallet af lejlighedsvist gæstende fugle (firkanter) samt af fugle, der slet ikke blev set skønt de var i live (fyldte cirkler).

Results

Population and number of ringed geese

From the data in *GsArkiv* the number of ringed geese each year can readily be extracted. The number of geese encountered regularly during the season is given in Fig. 2 (top graph), with paired birds and singles shown separately. In addition, each year some birds were encountered only occasionally. These apparent visitors (of which some became regulars in later years or had been so previously) are shown in the bottom graph of Fig. 2, as are birds that were not seen but are known to have been alive since they were seen or recovered later.

There is no direct information on the number of unringed geese. For the paired geese, however, it is possible to make a rough estimate of the total number based on the number where only the female, only the male, or both were ringed, assuming that ringed and unringed birds associated at random. The result, and the inferred estimate of the proportion of paired female and male geese that were ringed, appear from Fig. 3 and Fig. 4. Jensen (1977) estimated the proportion of ringed birds during 1963-1976 at 37% (with annual values ranging between 26-47%) by repeated counts from the arrival of the geese until early July, but did not distinguish between females and males, or between breeders and non-breeders.

From Fig. 3 it appears that the population at Utterslev Mose was fairly constant during the sixties, with some fluctuation and apparently a weakly increasing tendency to about 100 pairs. It then dropped by a third in the early seventies, but quickly returned to and even surpassed its former level before the end of the decade. The early eighties saw a new decline, this time by almost 50%, after which the population started to increase faster than ever before and continued to do so till the end of the study, only interrupted by minor, temporary setbacks in 1988 and 1993.

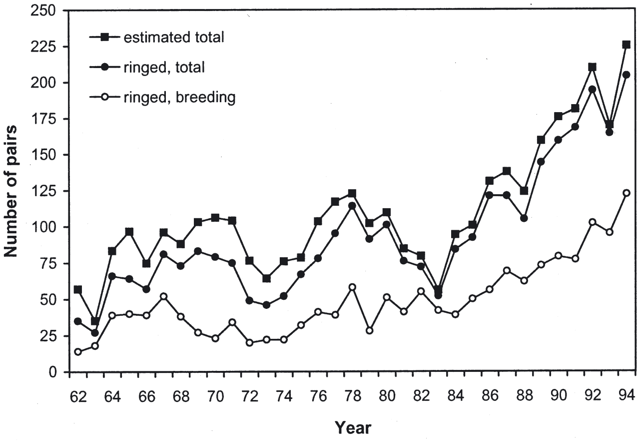
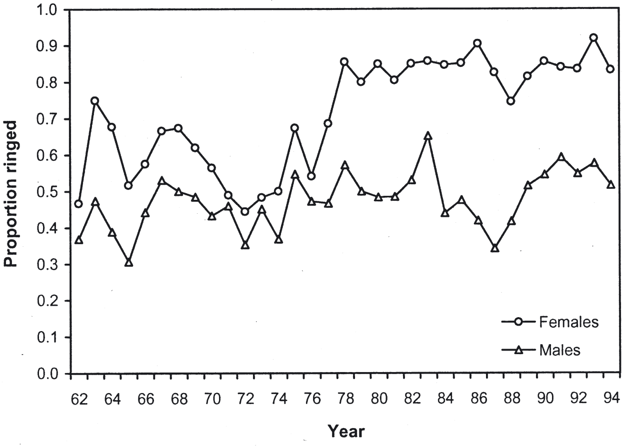


Fig. 3. The total number of Greylag Goose pairs in Utterslev Mose during 1962-1994, estimated from the number of ringed and unringed pair members in pairs with at least one ringed member. The number of these ringed pairs is also shown, as well as the number of them that bred.
Antallet af par i Utterslev Mose 1962-1994. Fyldte cirkler viser "kendte" par, dvs. med én eller begge mager ringmærkede, mens fyldte firkanter viser det totale antal par, estimeret ud fra antagelsen at mærkede og umærkede fugle parres tilfældigt. Desuden er vist antallet af kendte par, der forsøgte at yngle (åbne cirkler).

Fig. 4. The estimated proportion of paired Greylag Geese present in Utterslev Mose that wore rings during any year of the study period.
Den estimerede andel af de tilstedeværende gæs i Utterslev Mose, der havde ring i undersøgelsesårene. Cirkler viser hunner, trekanter hanner.



Ring recoveries

A total of 1165 of the ringed geese have been recovered dead between the breeding seasons 1959 and 1995, i.e., from the start of the study until one year after the last batch of goslings were ringed. 148 had been ringed as adults and 1017 as goslings. Very nearly half of the latter (507) were found during their first year of life, the remaining 510 one or more years after ringing. A large majority (1003) was reported shot, 432 1st-year birds and 571 older birds (442 ringed as goslings, 129 ringed as adults). In other words, a minimum of 86.1% of the recovered birds were shot, with very little variation between the three groups (G_2 = 0.61, P = 0.74).

Except for 35 recoveries (12 first-years) reported from Norway, Sweden, Finland, Poland, Germany, Belgium and Portugal, all were found in Denmark, Netherlands, France or Spain. Of the 1130 birds recovered in these four countries, 977 were reported shot. Their distribution over time and country is shown in Fig. 5. There was marked variation in the proportions reported from each of the four countries, cf. the bottom graph in the fig-

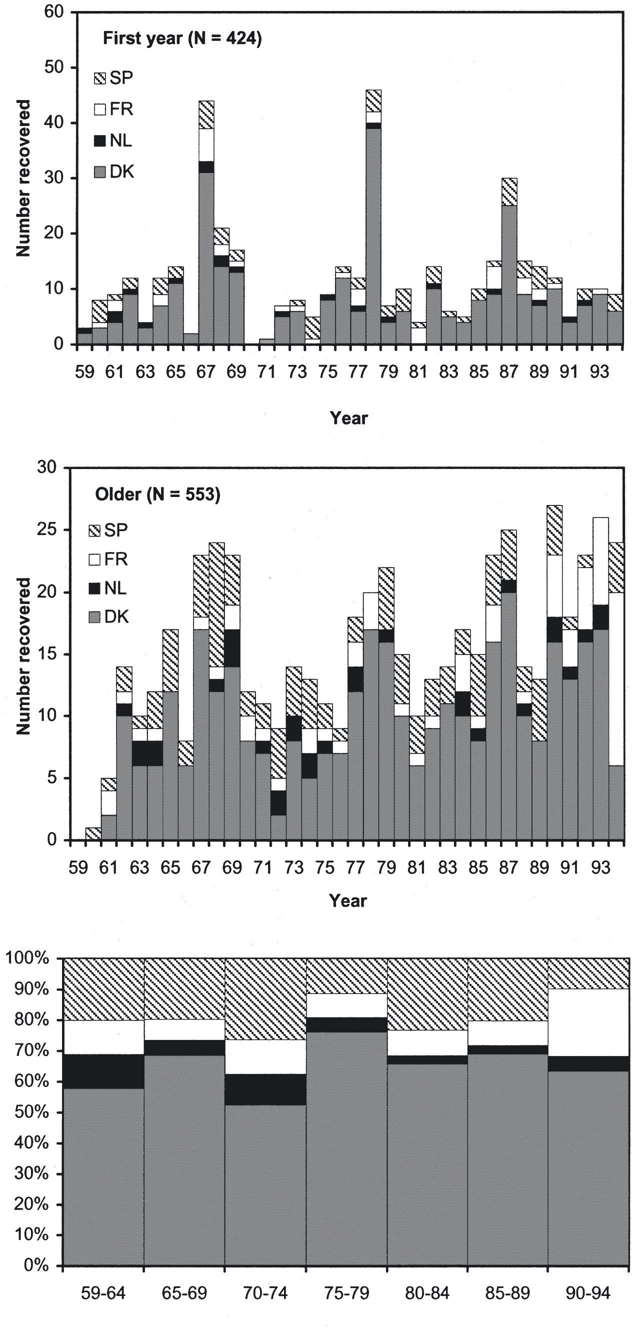


Fig. 5. Ringed Greylag Geese recovered as shot during the study period (including the first part of 1995). The numbers shown in each column refer to recoveries between the breeding season in the indicated year and the breeding season in the following year. The countries are Denmark (DK), Netherlands (NL), France (FR), and Spain (SP). Not shown are 8 juveniles and 18 older birds recovered in Norway, Sweden, Finland, Poland, Germany, Belgium, and Portugal. The bottom graph shows the distribution of recoveries (both age-classes combined) on the four countries, averaged over 5-year periods (country signatures as in top and centre graph).
Grågæs fra Utterslev Mose genmeldt (skudt) mellem ynglesæsonen det angivne år og ynglesæsonen det følgende år. De angivne lande er Danmark (DK), Holland (NL), Frankrig (FR) og Spanien (SP) (kun i alt 26 fugle blev skudt uden for disse fire lande). Øverst: første leveår. I midten: ældre fugle. Nederst: procentdel fra hvert af de fire lande, vist som fem-årige gennemsnit.

ure. A G-test with 4 countries, 7 periods, and 2 age-classes (1st year, older) confirmed a strong heterogeneity ($G_{39} = 83.57$) which could be partitioned into a time effect ($G_{18} = 56.14$, $P = 10^{-7}$), a non-significant age effect ($G_3 = 6.11$, $P = 0.11$), and the interaction between time and age ($G_{18} = 21.32$, $P = 0.26$).

Photo: Vibeke Tofte.

Phenology: Spring arrival, and emergence of goslings

Arrival dates of breeders and one year old immatures are shown in Fig. 6 (all years combined) and Fig. 7 (annual means). Age-specific mean dates and extremes are given in Table 2. Breeders are geese who laid, or whose female partner laid, irrespective of the success of the breeding attempt. The few birds recorded already on the first day of the year are omitted from Fig. 6, but even those seen later in January had probably overwintered at Utterslev Mose or some nearby locality.

The yearlings arrived significantly later than older birds, and over a longer time interval, and similar differences – although to a smaller extent – even existed between 2 and 3 year old birds, and between 3 year old and older birds (Table 3). There was little difference between birds 4+ year old and birds ringed as adults as regards mean date of arrival, but the variance was slightly higher in the 4+ year olds. In addition, there seems to be some difference in arrival between females and males, especially non-breeders, as shown in Tables 4-5 for all geese reliably sexed at Utterslev Mose at some time during their life span. Specifically for the yearlings, of which several were never sexed with certainty because they were not re-sighted in later years, those sexed as males at ringing had more dispersed arrival dates than those sexed as females ($F_{410,663} = 1.49$, $P < 10^{-5}$), although the difference in arrival date was not significant (females 6 Apr, males 8 Apr, $t' = 0.79$, $P = 0.43$).

The dispersal in arrival dates as shown above was partly an effect of combining different years, but generally it was considerable in any given year (annual standard deviations about 21 days both for yearlings and for birds 4 years or older). The difference in mean date between years was highly significant (two-way ANOVA with year and breeding status as factors, $P < 10^{-50}$ or smaller for different subgroups of females (all, adults, breeders hatching young)). For breeding status the significance was even stronger (all females: $P < 10^{-150}$; cf. also Table 4), and owing to the relationship between breeding status and age this is partly a restatement of the relationship between arrival date and age shown in Tables 2-3. If only the adult females were considered (4+ year olds as well as birds ringed as adults), the relationship between status and arrival date was still strong ($P < 10^{-18}$), but the interaction with year disappeared ($P = 0.26$, compared with $P < 10^{-10}$ for all females).

Even if the sample was limited to females hatching young (status 4 and 5, cf. Table 4), some relation between status and arrival date remained ($P = 0.004$), cf. that status-4 birds on average arrived 3 days *earlier* than status-5 birds (Table 4). This difference was significant for females ($t_{756} = 2.56$, P

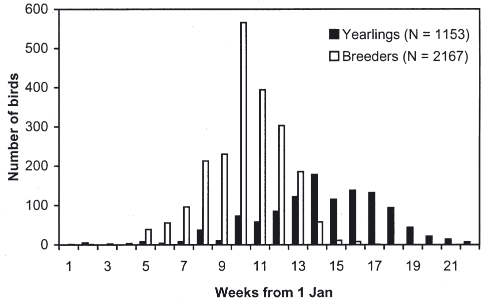


Fig. 6. Spring arrival (date of first sighting) of Greylag Geese in Utterslev Mose, combined for all years during 1963-1994. Shown are one year old immatures and birds that initiated breeding later in the season. Nonbreeding birds aged two years or more had intermediate arrival dates (see text).
Ankomstdato om foråret for 1-årige fugle (sorte søjler) og fugle, der ynglede senere samme år (hvide søjler). Ikke-ynglende 2-årige og ældre fugle havde ankomstdatoer, der lå mellem datoerne for de to viste grupper. Ankomster kombineret for alle årene 1963-1994.

= 0.01), but not quite for males (t_{513} = 1.75, P = 0.08). Why birds that arrive early should be more prone to lose their goslings is difficult to understand, and quite likely the effect is spurious. It might, for example, have been caused by birds belonging to the two status classes on average representing different years, but that does not seem to be the case (cf. also the ANOVA result), and years where particularly many pairs lost their goslings were not, as a rule, early years.

The timing of arrival to the breeding grounds could be influenced by conditions in the winter quarters, for example through the nutritional condition of the birds. However, a more direct connection with factors in the general breeding area, or in nearby staging areas, is perhaps more likely, at least in most years. For the Utterslev Mose geese there is a clear negative correlation between arrival date and March mean temperature for Denmark, for both age-groups illustrated in Fig. 7: yearlings r = -0.619, P = 0.0002; 4+ year old birds r = -0.503, P = 0.0046. The correlation with the February mean temperature is even better for the yearlings (r = -0.674, P = $3 \cdot 10^{-5}$), but not quite significant for the older birds (r = -0.344, P = 0.063).

Annual mean arrival dates are shown in Fig. 8 for birds that bred later in the same season. A negative trend over time is suggested but not quite significant (r = -0.330, n = 32, P = 0.065). With individual birds as the unit of observation, the trend is highly significant (r = -0.253, n = 2173, P = $4 \cdot 10^{-33}$), but the main reason for this is the high number of birds in the last few, relatively early years. Almost identical results are obtained for yearlings (annual means: r = -0.259, P = 0.15; individual birds: r = -0.156, P = $9 \cdot 10^{-8}$).

There is a close correlation between annual mean arrival date (Fig. 8) and appearance of broods (Fig. 9) (r = 0.774, P = $2 \cdot 10^{-7}$). The first goslings usually appear around 20 April, although exceptionally, broods have been seen as early as 9 April. The mean date for 939 broods during 1962-1994 was 6 May. Considering the close relationship with spring ar-

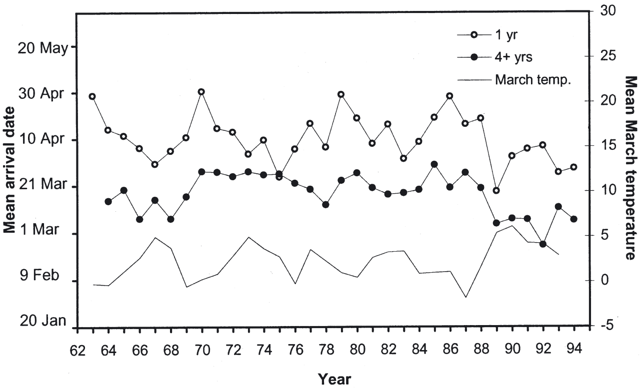


Fig. 7. Mean spring arrival dates of Greylag Geese in Utterslev Mose, 1963-1994, shown for birds aged one year and four years or more, respectively. The mean March temperature is shown for comparison (from Rosenørn & Lindhardt 1993).
Årlige, gennemsnitlige ankomstdatoer for 1-årige fugle (åbne cirkler) og fugle mindst 4 år gamle (fyldte cirkler). Nederst er vist gennemsnitstemperaturen for marts det pågældende år.

Table 2. Mean arrival dates of ringed Greylag Geese to Utterslev Mose, 1963-1994. Birds ringed as goslings are grouped according to age (years). Sample sizes refer to bird-seasons, i.e. each bird is included every year it was recorded. Sample size for earliest/latest mean dates range from 15-151.
Dato for Grågæssenes ankomst til Utterslev Mose, 1963-1994. Unge-mærkede fugle er opdelt efter alder (år). Ud over gennemsnittet for alle årene under ét, er vist den tidligste ('earliest') og den seneste ('latest') af de årlige gennemsnitsdatoer.

	Ringed as goslings				adults
	1	2	3	4+	
Mean date	8 Apr	21 Mar	18 Mar	16 Mar	15 Mar
earliest	18 Mar	5 Mar	24 Feb	26 Feb	28 Feb
year	1989	1966-68	1990	1992	1992
latest	30 Apr	15 Apr[1]	16 Apr	31 Mar	7 Apr
year	1970	1963	1971	1985	1972
st.dev. (days)	26.42	23.39	24.63	23.34	22.07
n	1178	888	656	1589	1077

[1] 25 Apr in 1982, but based on only 7 birds

Table 3. Statistical significance of differences in mean arrival dates and variances between the age-groups shown in Table 2. Since variances differ, the comparisons of means are repeated using t', as suggested by Sokal & Rohlf (1981).
Signifikansniveauer P (to varianter), når ankomstdatoerne for forskellige aldersgrupper sammenlignes. Sammenholdt med datoerne i Tabel 2 ses, at 1-årige ankommer senere end 2-årige, som kommer senere end 3-årige. Det ser også ud til, at de 3-årige kommer en smule senere ældre fugle, mens der ingen forskel i ankomsttidspunkt er mellem adult-mærkede og ældre unge-mærkede fugle – men spredningen er større hos sidstnævnte (F-test). De midterste søjler angiver hvor mange år ud af 32, de 1-årige kom senere end de 2-årige, osv., og i hvor mange af disse år forskellen var signifikant.

	t	df	P[1]	yrs a>b[2]	signif. yrs[3]	F-test	t'	P[1]
1 vs 2	16.21	2064	0	31	21	0.00006	16.49	0
2 vs 3	2.17	1542	0.030	22	7	0.076	2.15	0.03
3 vs 4+	2.04	2243	0.042	16	6	0.049	1.99	0.047
4+ vs ad.	0.36	2664	0.717	20	2	0.023	0.37	0.72

[1] $P=0$ means $P<10^{-50}$

[2] meaning years (of 32) in which mean date of 1-years was later than mean date of 2-years, etc.

[3] no. of years (out of 32) in which the difference was significant ($P<0.05$)

Table 4. Mean arrival dates of female and male Greylag Geese to Utterslev Mose, 1963-1994. Breeding status codes are: 1: not paired, 2: paired, not breeding, 3: laying, not hatching, 4: hatching, not fledging, and 5: fledging goslings. The 'all' samples include some birds of unknown status. See Table 5 for tests of differences between sexes.
Gennemsnitlige ankomstdatoer for hunner ('females') og hanner ('males'), afhængigt af ynglestatus (1 enlig, 2 udparret men ikke ynglende, 3 fik æg men ikke unger, 4 fik unger men mistede dem, 5 fik flyvefærdige unger).

	Breeding status					all
	1	2	3	4	5	
Females	3 Apr	20 Mar	10 Mar	7 Mar	10 Mar	19 Mar
st.dev.	23.12	21.53	13.99	13.62	13.63	21.48
n	563	1136	574	133	625	3103
Males	7 Apr	26 Mar	9 Mar	7 Mar	10 Mar	21 Mar
st.dev.	32.23	29.09	16.57	13.36	15.71	27.90
n	258	656	322	72	443	1832

Table 5. Statistical significance of differences between sexes in mean arrival dates and variances, as shown in Table 4. t': comparison of means of samples with different variances, cf. Table 3.
Tests af kønsforskellene i ankomstdato vist i Tabel 4: P (to varianter) angiver signifikansniveau ved sammenligning af datoer, F-test ved sammenligning af spredninger.

Status	t	df	P	F-test	t'	P
1	1.73	819	0.084	10^{-10}	1.53	0.12
2	4.85	1790	10^{-6}	10^{-18}	4.48	0.00001
3	-1.15	894	0.250	0.0002	1.10	0.27
4	-0.06	203	0.953	0.416	-0.06	0.95
5	-0.02	1066	0.981	0.0006	0.02	0.98
all	3.59	4933	0.0003	10^{-37}	4.44	0.00001

rival, it is not surprising that even here a negative trend is suggested but not significant (Fig. 9; r = -0.331, n = 33, P = 0.060). Based on individual broods, the trend is highly significant (r = -0.198, n = 939, $P = 9 \cdot 10^{-10}$), because the number of broods was high during the last few years where 1989-1992, following four unusually mild winters in succession, were particularly early (mean 28 April). The only other years with mean date 1 May or earlier were 1967 and 1973-1975.

Sexing goslings

The method used to estimate probabilities of mis-sexing is presented in Appendix 1. For the entire sample (1959-1993) it appears that approximately 10% of the goslings were mis-sexed, with little difference between females and males (Table 6). The estimates of the 'probability of being mis-sexed' (the probability that the sex-score at ringing of a randomly chosen 'adult' bird turns out to be in error) are similar if the entire population is considered (due to the approximately even sex ratio), but about twice as high for birds scored as males, and half as high for birds scored as females, when only returned birds are considered, reflecting the sex-bias in return probability.

It may be assumed that the 'quality' of sex determinations varied between ringing occasions, adding to the random variation between samples. Numbers from single years are small, however, making it difficult to distinguish poor sexing from random fluctuation. The total sample of mis-sexed birds among those that returned and were sexed as adults is only 89 (27 males identified as females at ringing, 62 females taken for males). Three years

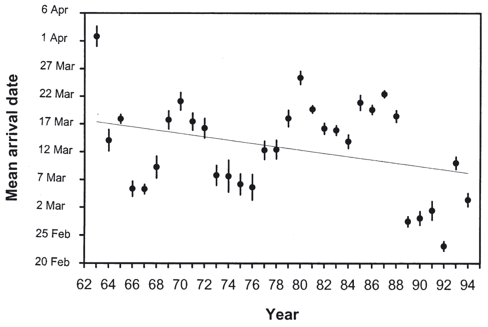


Fig. 8. Mean arrival day to Utterslev Mose of breeding Greylag Geese, 1963-1994. Error bars show standard errors. The negative trend is not quite significant (see text).
Gennemsnitlig ankomstdato (med angivet usikkerhed) for ynglefuglene. En tendens mod tidligere ankomst gennem perioden er antydet, men statistisk ikke helt signifikant.

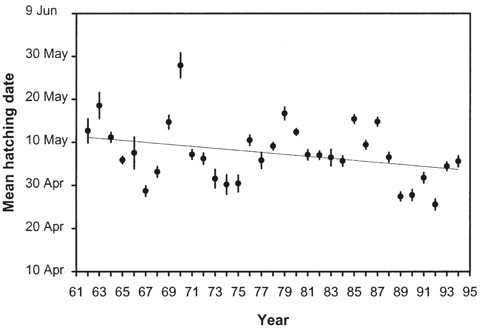


Fig. 9. Mean 'hatching' date of broods in Utterslev Mose, 1962-1994 (the day when the broods were first seen). Error bars show standard errors. The negative trend is not quite significant (see text).
Gennemsnitlig klækningsdato, med angivet usikkerhed. En tendens mod tidligere ankomst gennem perioden er antydet, men statistisk ikke helt signifikant.

Table 6. Sex ratios and estimated reliability of sex determination of goslings in three subperiods and throughout the study period (cf. Appendix 1). Estimates of actual numbers of females and males do not add up exactly because numbers have been rounded off.
Fejlprocent ved kønsbestemmelsen af gæslinger, vurderet på basis af de fugle, der overlevede og senere kunne kønsbestemmes med sikkerhed (jf. Appendix 1). For materialet som helhed er ca 10% fejlbestemt (uanset køn). Yderste højre søjle viser andelen af de tilbagevendte fugle, der var blevet fejlbestemt som gæslinger. Fordi næsten alle overlevende hunner, men kun nogle hanner vender tilbage, er andelen af fejlbestemt 'hunner' (altså i virkeligheden hanner) mindre end de 10%, mens andelen af fejlbestemte 'hanner' er større.

		Number scored	Number estimated	Prob. of mis-sexing	Prob. of being mis-sexed [1]
1959-70	Females	204	220	0.120	0.029
	Males	222	206	0.049	0.188
1971-80	Females	376	363	0.110	0.076
	Males	378	391	0.135	0.190
1981-93	Females	866	869	0.094	0.039
	Males	914	911	0.086	0.193
1959-93	Females	1446	1451	0.099	0.046
	Males	1514	1509	0.096	0.191

[1] refer to the returned sample and to sex as scored at ringing, i.e., the probability that a returned bird originally scored as a female is actually a male, and that a returned bird originally scored as a male is actually a female, respectively

had both a high error rate and a fairly high number of goslings, together according for 21 of the mis-sexed birds: 1977 (36 returned goslings, 8 mis-sexed), 1986 (23, 4), and 1993 (50, 9); in the last case, however, 'true' sex may be unreliable since it could only be assessed in one year, and on basis of yearling immatures. More generally, estimates for different subperiods (decades) during the study suggest that the error rate was slightly higher in the seventies than in later years (Table 6).

The original and 'corrected' sex ratios (Table 6) suggest a small bias towards males in goslings produced at Utterslev Mose. However, the deviation from an 1:1 ratio was not significant (P = 0.21) even in the entire sample, where the test had maximal power.

Return and survival

There is good reason to believe that geese staying at Utterslev Mose during any given year (season) were also recorded during that year, usually a good number of times. For birds properly belonging to the UM community, hence, the proportion of those recorded in year i that were re-sighted in year i+1 should be a reliable measure of survival during the intervening year. However, to correct for birds that skipped a year the best estimate would be the proportion known to be alive, rather than the proportion re-sighted.

As will be seen, annual survival of older birds can apparently be estimated with good precision in this way. For younger birds, especially those in their first year of life but to some extent also the next few age-classes, other methods are desirable, because not all survivors will turn up at UM at all, or do so as youngsters only. Information on such 'emigrants' mainly comes from ringing recoveries which might ideally be included in the analysis by applying maximum likelihood techniques available in the software package MARK (Cooch & White 2002). However, it turns out to be difficult to reconcile some characteristics of the goose population of Utterslev Mose with any of the models in MARK, making the interpretation and evaluation of the results problematic. These analyses are therefore omitted from the main text, but are briefly presented in Appendix 2 together with a discussion of the involved problems.

Return pattern

Of the ringed goslings (cf. Table 1), 1580 (46% of those ringed before 1994) are known to have survived for at least one year. Of these, 1415 were identified at Utterslev Mose during one or more seasons, and the remaining 165 are known to have survived because they were recovered after at least one year.

A minor proportion (53) of the returning geese appeared to be occasional visitors to UM only, because they were only infrequently seen during any of the seasons where they were known to be alive. A few others apparently were absent for two or more years in succession and could hence be assumed to have emigrated (24), immigrated (8), or emigrated but later returned after two or more years (6). For an additional five birds the pattern was more difficult to interpret, and some or all of these birds may have been in poor health. The remaining 1319 birds were classified as 'regular' at Utterslev Mose. This classification was of course rather uncertain for birds only surviving for a few years, and since birds were regarded as 'regular' unless good reasons indicated otherwise, this group may be somewhat inflated. The sex-distribution of the returned birds is shown in Table 7, and the fairly large proportion of birds in the 'regular' group that was never reliably sexed mainly consists of such (apparently) short-lived birds.

Table 7 shows that many more females than males return to UM. If only reliably sexed birds are considered, the proportion of females exceeds two thirds (69%), despite the almost even sex ratio among the goslings. In other words, the probability that a bird returns is more than twice as high for females as for males.

Table 7. Occurrence pattern in Utterslev Mose of 1580 geese ringed as goslings and known to have survived for one or more years.
Forekomstmønster i Utterslev Mose af Grågæs mærket som gæslinger. Alle viste fugle overlevede mindst ét år, men nogle blev aldrig kønsbestemt som voksne (søjlerne 'assumed'). Regnet oppefra viser de tre rækker fugle, der aldrig eller næsten aldrig blev set (som regel genmeldte fugle), fugle der som voksne ud- eller indvandrede fra/til UM, og fugle der optrådte regelmæssigt hele livet. Females = hunner, males = hanner, unknown = ikke kønsbestemt.

	Females			Males			unknown sex	Total
	certain	assumed [1]	total	certain	assumed [1]	total		
Never or rarely seen	4	38	42	22	114	136	40	218
Emi- or immigrant	22		22	20		20	1	43
Regular	669	164	833	296	155	451	35	1319
Total	695	202	897	338	269	607	76	1580

[1] sexed at ringing only

Table 8. Percent of birds known to be alive but not recorded in Utterslev Mose in any given year, according to age, sex and pattern of occurrence in Utterslev Mose. Numbers refer to bird-seasons.
Andelen (%) af fugle, der skønt i live ikke blev set i Utterslev Mose i ethvert givet år. Fuglene er opdelt på otte aldersklasser, og for hvert af de to køn vises både det fulde materiale og de regelmæssigt optrædende UM-fugle. Meget få af disse egentlige UM-fugle springer et år over, når de først har nået en alder på 2-3 år (hunner) hhv. 5-6 år (hanner).

	Age of bird (years)								Total
	1	2	3	4	5	6	7	8+	
All									
pct absent	25.1	15.9	15.5	17.7	16.2	16.2	17.1	15.0	18.7
n	1580	1088	783	582	439	296	187	433	5388
All Females									
pct absent	15.9	3.2	2.2	3.8	2.7	4.4	5.4	11.0	6.9
n	694	598	455	344	263	183	112	263	2912
Regular Females									
pct absent	15.1	2.4	0.7	1.2	0.4	0.6	2.0	0.9	4.7
n	669	573	430	321	242	165	101	217	2718
All Males									
pct absent	23.7	10.0	10.8	16.5	16.7	18.0	21.3	11.8	15.8
n	338	291	213	164	126	89	61	152	1434
Regular Males									
pct absent	20.9	5.6	4.6	4.8	3.3	1.6	0.0	1.9	8.4
n	297	251	173	125	91	62	36	104	1139

In all years some of the geese known to be alive failed to turn up at UM (Table 8). This held true even for birds considered 'regular' UM-geese, especially during the first years of life. Among 'regular' females, 15% were absent when one year old and 2-3% when two years old, but very few thereafter. Corresponding numbers for 'regular' males were somewhat higher and waned more slowly with age (females vs males 1 year old $G_1 = 4.75$, $P = 0.029$; 2-4 years $G_1 = 4.55\text{-}9.31$, $P = 0.002\text{-}0.033$). The proportion of absent birds naturally increased when even the 'irregular' UM-birds were included in the sample, and the effect was more pronounced in males than in females, so that the sex difference was further emphasized (yearlings $G_1 = 8.97$, $P = 0.0027$; 2-4 years $G_1 = 16.36\text{-}27.91$, $P = 10^{-4} - 10^{-7}$).

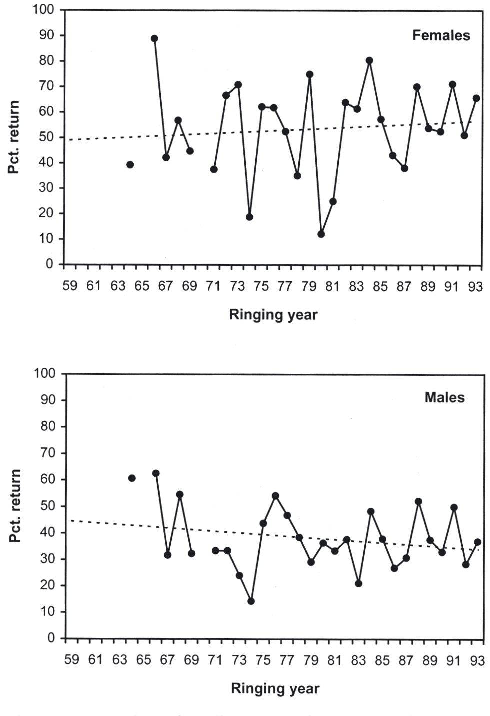


Fig. 10. Proportion of goslings returning to Utterslev Mose after one or more years, or otherwise known to have survived their first winter. The assignment to sex is taken from the ringing records and are not correct for all birds (see text). Goslings were not sexed in 1959-63 and 1965. *Andelen af de ringmærkede gæslinger, der senere er vendt tilbage, eller på anden måde vides at have overlevet første år (fx fordi de siden er genmeldt). Det angivne år er "startåret", dvs. ringmærkningsåret. Kønnet er angivet som det blev bestemt ved ringmærkningen, og er derfor ikke korrekt for alle fugle. Da kun få hunner emigrerer, er grafen her et mål for overlevelsen, mens den for hannerne viser den kombinerede effekt af død og emigration.*

Cases where older birds were absent from UM often concerned the last season in the life of the bird. Some birds may stay away from the breeding site if they are ill or wounded, which could also make them more vulnerable to shooting. The only birds known with certainty to have died are those reported shot or found dead of other causes. Of 306 such birds more than two years old (170 females, 136 males), including geese ringed both as goslings and as adults, 51 (22 females, 29 males) had been absent in their last spring, corresponding to 16.7% (females 12.9%, males 21.3%). These figures are higher than the proportion expected to be absent in any given year, 4.5% for females and 14.7% for males (cf. Table 8, all females and all males, age >2 years), the difference being statistically significant for females ($G_1 = 16.51$, $P = 0.00005$), but not quite for males ($G_1 = 3.65$, $P = 0.06$). Of 'regular' birds ringed as goslings and more than two years old, 5 (4.6%) of 109 recovered females, and 9 (19.6%) of 46 recovered males had been absent in the previous season; the corresponding figures for regular geese in Table 8, averaged for the same age-classes, are for females 0.9% ($G_1 = 3.65$, $P = 0.06$), and for males 3.4% ($G_1 = 15.61$, $P = 0.0001$).

Return rates of yearlings

The proportion of goslings known to have survived their first winter was 46.4% (1580 out of 3403, cf. Tables 1 and 7).

The proportion of sexed goslings known to have survived is shown in Fig. 10. It appears that there is a considerable among-year variation, which probably in part reflects real variations in survival and fidelity to natal site, but to some extent must also be random (mean number of goslings ringed was 51.6 ± 29.8 SD females and 54.1 ± 31.9 males). In addition to this variation, a positive trend over time is suggested for females, and a negative trend for males, but neither comes close to statistical significance (females: $r = 0.10$, $P = 0.61$; males: $r = -0.23$, $P = 0.25$).

Overall, 54.1% of the females returned, but only 39.3% of the males (Table 9). It must be borne in mind, however, that the determination of the sex of the goslings was imperfect, and that roughly 5% of the returning 'females' were in fact males, and 20% of the returning 'males' were females (Table 6). A coarse correction using these figures suggests that about 59% of (true) females, and 34% of males, did survive, which is borne out by the more formal correction shown in Table 9. For the females this might be a fairly good estimate of the mean first-year survival, but for the males it is cer-

Table 9. Number of Greylag goslings ringed in different subperiods and throughout the study period, and number known to have survived for one or more years ('returned'). Subdivision by sex as scored at ringing (*) is shown along rows, subdivision by 'true' sex (determined for adults) along columns. Goslings scored as probable females or males are pooled with the unknowns. Return rates are shown both according to sex score at ringing and to 'true' sex.
Unge-mærkede Grågæs, som overlevede mindst ét år, og andelen i forhold til antallet af mærkede ('return rate'). Køn (females = hunner, males = hanner) er angivet som bestemt ved mærkningen (rækker) eller senere konstateret med sikkerhed for voksne fugle (søjler). Dog viser den yderste højre søjle den estimerede 'return rate' for rigtige hunner (hanner). For hunner er 'return rate' næsten det samme som overlevelsen, og den ses at vokse gennem perioden. For hanner ses en faldende tendens, åbenbart fordi en stigende andel slår sig ned andre steder end i Utterslev Mose.

	Ringed	Returned				Return rate [1]	Return rate [2]
		Females	Males	unknown	Total		
1959-1970							
Females*	204	66	2	31	99	0.485	0.500
Males*	222	9	39	53	101	0.455	0.407
unknown*	371	56	44	63	163		
Total	797	131	85	147	363		
1971-1980							
Females*	376	121	10	50	181	0.481	0.551
Males*	378	15	64	73	152	0.401	0.344
unknown*	39	10	3	6	19		
Total	793	146	77	129	352		
1981-1993							
Females*	866	367	15	120	502	0.580	0.640
Males*	914	38	159	145	342	0.374	0.322
unknown*	33	12	2	7	21		
Total	1813	417	176	272	865		
1959-1993							
Females*	1446	554	27	201	782	0.541	0.593
Males*	1514	62	262	271	595	0.393	0.342
unknown*	443	78	49	76	203		
Total	3403	694	338	548	1580		

[1] Returns of birds sexed as females (males) at ringing

[2] Returns of 'true' females (males), estimated using number of 'true' females and males ringed (Table 6), and assuming that the sex distribution of returned birds of unknown sex was the same as of sexed birds (e.g., that $31 \cdot 66/68$ of the 31 unsexed birds in the first row were females, etc.)

tainly far below the real value and reflects that males are much less liable to return to the natal area than females are.

The tendency towards increasing return rates of goslings sexed as females becomes significant when grouping the years according to the subperiods in Table 9 ($G_2 = 6.89$, $P = 0.032$). The return rates in the rightmost column cannot be tested in any simple way, but since the trend is even stronger here, it would seem to be safe to conclude that first-year survival of females did indeed increase during the study period. The suggested decrease in return rates over time of goslings sexed as males cannot be confirmed in this way, however ($G_2 = 2.17$, $P = 0.34$). But since young males probably have about the same probability of surviving as young females, it looks as if an increasing proportion of the male goslings emigrated.

Return rates of adults

The goose population of Utterslev Mose appears to be almost closed as far as the females are concerned, except that a minor proportion of the female goslings may settle elsewhere without ever

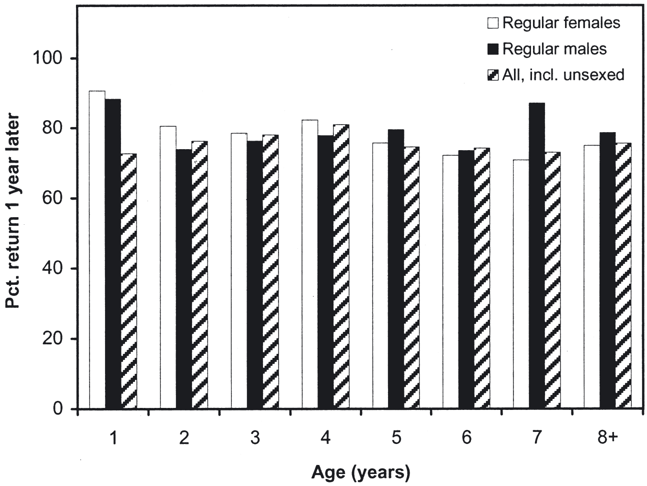


Fig. 11. Mean proportion of Greylag Geese that returned to Utterslev Mose the following year (or at least are known to have survived). Based on 632, 534, 409, 294, 218, 140, 96, and 199 goose-years (females); 284, 234, 164, 117, 78, 49, 31, and 98 (males); 1496, 1027, 746, 542, 397, 252, 174, and 405 goose-years (entire sample).
Andelen af Grågæs, der er vendt tilbage til mosen det følgende år, eller på anden måde vides at have overlevet. Den tilsyneladende overlevelse er vist for aldersklasserne fra ét til syv år, og for ældre fugle under ét, dels for sikkert kønsbestemte fugle (hunner (hvide søjler), hanner (sorte søjler)), dels for samtlige fugle (skråskraverede søjler; incl. nogle, der ikke blev kønsbestemt som voksne). Den påfaldende høje "overlevelse" af de yngste hunner og hanner er et artefakt.

turning up at UM, or after having spent a year as pre-breeders there. Besides, most of the female geese were ringed (Fig. 4), and the proportion of the present geese that was re-sighted can be assumed to have been close to 100 %, at least among the 'regulars'. It is therefore likely that the return rate provides a good estimate of the survival between years, and this may also be the case for 'regular' males, since these appeared to stay at UM even if they lost their mate and re-paired.

The selection of the sexed sample unfortunately introduces a bias in favour of long-lived birds, since the geese could usually be reliably sexed only when paired. The effect is evident when comparing the return rates for all UM geese combined (irrespective of sex and hence including unsexed birds) with return rates for reliably sexed 'regular' females and males (Fig. 11). For the total sample the return rates increase slightly and peak at the age of four years, after which they remain almost constant (if an increasing number of the youngest age-classes are deleted, the homogeneity improves abruptly when reaching four years: P = 0.009-0.12 if 0-3 age-classes are omitted, P = 0.93 if 4 classes are omitted, G-test). For the female sample, the survival from age 1 to 2 years is artificially elevated by the indirect selection of long-lived birds, and the same may hold true to a smaller extent even for the next few age-classes. Even here a small peak at 4 years is apparent, and some heterogeneity is suggested until the first four age-classes are disregarded ($P = 10^{-11}$-0.08 when 0-3 classes are omitted, P = 0.77 when 4 classes are). For males the picture is very similar except that no peak is apparent at 4 years, and the heterogeneity disappears completely when only the first age-class is omitted (P = 0.002 with all classes included, P = 0.67 when the first class is omitted).

The mean return rates in Fig. 11 are 0.757 ± 0.028 SD for the entire sample (n = 8 age-classes, based on 5039 goose-years), for the 'regular' females 0.782 ± 0.064 (2522 goose-years), and for the 'regular' males 0.794 ± 0.056 (1055 goose-years). Owing to the lack of homogeneity and the artificially elevated return rates of young age-classes these figures have limited value, however. For birds 5 or more years old the corresponding figures are 0.743 ± 0.011 (whole sample), 0.734 ± 0.023 (females), and 0.797 ± 0.056 (males). The difference between sexes is almost, but not quite significant ($t_6 = 2.07$, P = 0.08).

In all three samples there was a rather considerable variation over time, with much fluctuation, a distinct increasing tendency since the late sixties, and a few marked peaks and troughs. This is shown in Fig. 12 for sexed birds at least five years old. A trend was significant in females, and along the regression line (slope 1.0% per year) the return rate increased from 57.3% (1969) to 83.3% (1994). Although a trend was not quite significant in males, the corresponding figures for males were a slope of 0.7% per year and an increase from 67.7% to 85.6 %. Much of the fluctuation must certainly be noise, due to the limited sample sizes that remains when data are spread over 26 years – for the different years n = 23.9 ± 15.1 (females), 9.3 ± 5.2 (males). However, some peaks and troughs probably reflect actual good and poor years, for example 1981, known to have been a very bad year on the wintering grounds in Spain (see Discussion) and also marked by a decline in the Utterslev Mose population (Fig. 3).

The mean of the annual return rates in Fig. 12, weighted according to number of birds contributing to the estimate, is 0.741 ± 0.110 for the females, 0.793 ± 0.135 for the males. In this case the effective size of the samples is not clear, but the significance can be tested by contingency analysis (Table 10). Although a difference between sexes is suggested, it is not significant (P = 0.10).

Geese ringed as adults and classified as 'regular' at UM had return rates varying over time, like those ringed as goslings (Fig. 13). Some of the peaks and troughs concern the same years as found in Fig. 12, for example the dip in the very poor year 1981. Even here an increasing tendency over time is suggested but does not attain statistical significance; the slopes of the regression lines are only 0.5% year^{-1} (females) and 0.2% year^{-1} (males). Weighted means of the return rates shown in Fig. 13 are 0.816 ± 0.135 SD for females, 0.822 ± 0.094 SD for males. The small difference between females and males is not statistically significant (Table 10).

Among adult-ringed females as well as among females ringed as goslings and more than four years old, the return rate was slightly lower for those that fledged a brood than for those that did not, but in none of the cases was the difference statistically significant (Table 11). In males the opposite tendency was found, and the difference between those fledging young and those not fledging young was significant in males ringed as adults. Despite the lack of significance this result may suggest a minor cost of breeding in females.

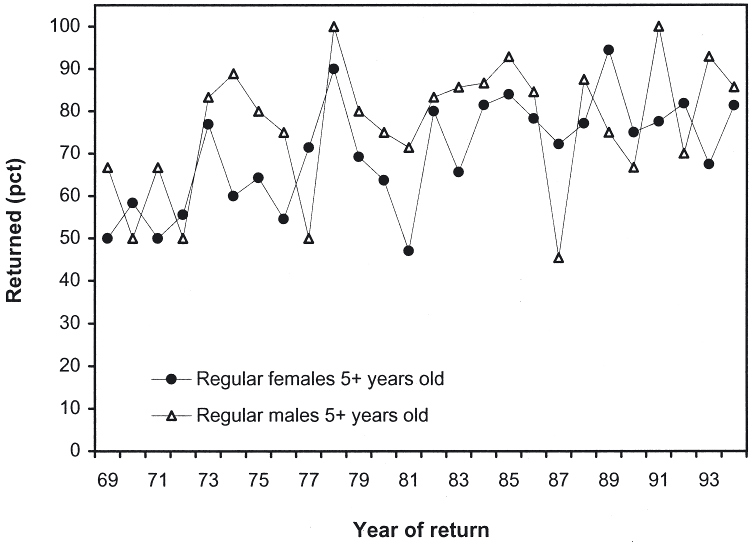


Fig. 12. Annual return rates for regular, sexed birds at least 5 years old (in the 'base' year). The first years (prior to 1969) are excluded because too few ringed birds were available. Mean return rate (percent ± SD) is 70.3 ± 12.7 (females) and 76.7 ± 15.2 (males). An increasing trend is significant in females (r = 0.625, P = 0.0006)) but not quite in males (r = 0.361, P = 0.07).
Årlig andel af voksne gæs, der er vendt tilbage til mosen det følgende år, eller på anden måde vides at have overlevet. Kun sikkert kønsbestemte, regelmæssige UM-fugle mindst fem år gamle er betragtet. Hunner: fyldte cirkler; hanner: åbne trekanter. Den stigende tendens gennem perioden er signifikant for hunner, men ikke helt for hanner.

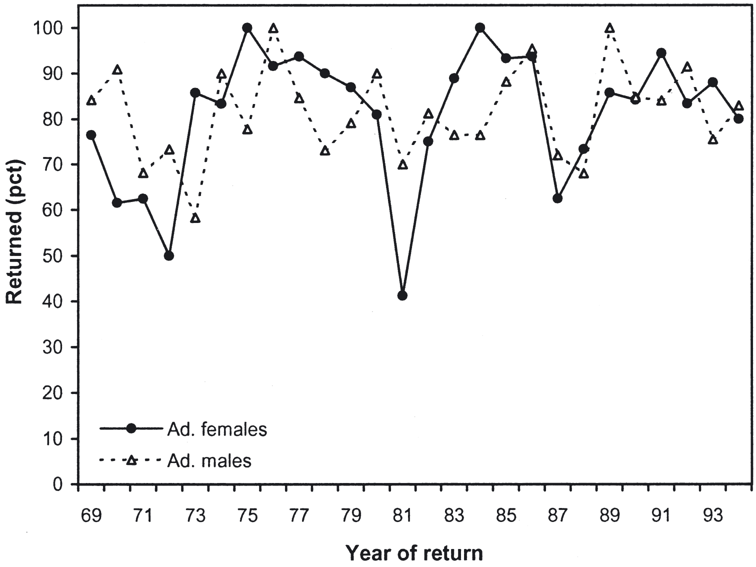
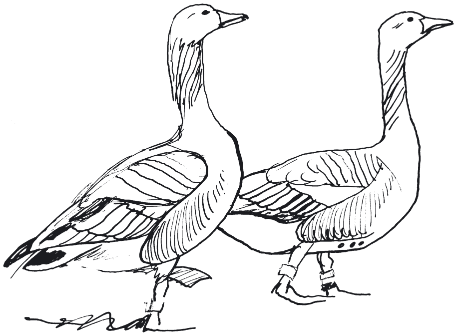


Fig. 13. Return rates of Greylag Geese ringed as adults and considered regular residents in Utterslev Mose. There is no statistically significant trend (females r = 0.26, P = 0.20; males r = 0.16, P = 0.43).
Som Fig. 12, men for fugle ringmærket som adulte. Der er ingen signifikant tendens.



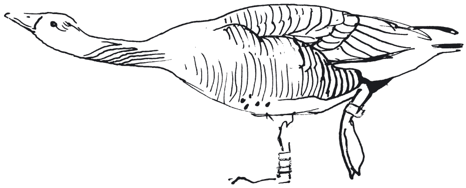


Table 10. Apparent survival of adult Greylag Geese in Utterslev Mose: returns from one year to the next, summed for 1969-1994. AF females ringed as adults, AM males ringed as adults, YF females ringed as goslings, YM males ringed as goslings. Birds ringed as goslings included only if at least five years old. All birds considered appeared to be UM residents throughout their life span.
Tilsyneladende overlevelse af adulte, regelmæssige UM Grågæs, baseret på hvor mange der vides at have overlevet ('returned') fra et år til det næste (summeret for 1969-1994). AF, AM: adult-mærkede hunner hhv. hanner; YF, YM: unge-mærkede hunner hhv. hanner, alle mindst fem år gamle. Testen under den vandrette streg viser, at adult-mærkede hunner overlevede bedre end unge-mærkede hunner, mens ingen af de øvrige sammenligninger var signifikante.

Group	AF	AM	YF	YM	YM
Total	385	639	621	242	242
Returned	314	525	460	192	192
Pct returned	81.6	82.2	74.1	79.3	79.3
Test	AF vs YF	AM vs YM	AF vs AM	YF vs YM	YF vs YM
G_1	7.669	0.907	0.059	2.676	2.676
P	0.006	0.341	0.809	0.102	0.102

Shooting mortality

The recovery rate is the proportion of ringed birds alive at the start of the period considered that are reported dead during the period. If this is modified to include only birds reported shot, the recovery rate provides a minimum estimate of the shooting mortality, the percentage of birds shot during the period. Generally a significant proportion of the shot birds are never reported, however, so the recovery rate substantially underestimates the shooting mortality.

Annual recovery rates can be calculated directly for first-year birds where the number of ringed birds alive at the start of the period is simply the number ringed. Dividing the recovery numbers shown in Fig. 5 by ringing numbers (Table 1) yields the recovery rates shown in Fig. 14, with standard errors (vertical bars) estimated using the binomial distribution. There is much variation overlaid by a decreasing trend. Along the regression line, the recovery rate drops from 0.183 in 1966 to 0.067 in 1994, with a mid-point at 0.125.

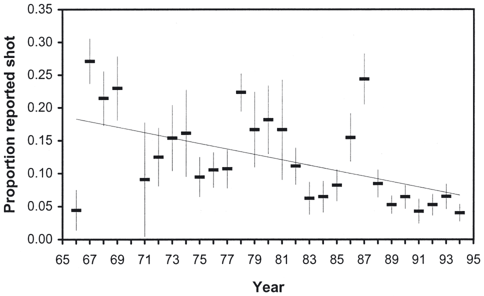


Fig. 14. Recovery rates for first-year birds (sexes combined) calculated directly as the proportion of the marked birds that was reported shot before the following spring. Error bars show standard errors obtained under the assumption of binomially distributed recovery numbers from each cohort. The regression line is added (r = -0.528, P = 0.001).
Årlig genmeldingsrate for førsteårs-fugle (procentdel af ringmærkede fugle, der er rapporteret skudt inden det følgende forår). Den faldende tendens gennem perioden er signifikant (r = -0,528, P = 0,001).

The proportion of goslings failing to return was shown above to be in the order of 45% for females and 60% for males, so 7-18% being reported shot may not look as very much. However, the number shot but not reported may well be of roughly the same magnitude as the number reported, and the fact that the recovery rate correlates well with the proportion of females failing to return (r = 0.445, P = 0.02) suggests that shooting was in fact a major mortality factor for young Greylag Geese during the study period. A similar correlation cannot be expected with males, because young males often fail to return even though they are still alive; and the correlation is indeed insignificant (r = 0.246, P = 0.22).

Table 11. Apparent survival (return probability) of 'regular' female and male Greylag Geese fledging or not fledging young. Birds ringed in Utterslev Mose, 1959-1993. Birds ringed as adults ('Adults') and as young and aged five years or more ('Young') are treated separately. Birds less than five years old are not considered.
Tilsyneladende overlevelse til det følgende år ('pct. return') af hunner ('females') og hanner ('males'), der hhv. fik og ikke fik flyvefærdige unger ('fledging', 'not fledging'). Adultmærkede ('adults') og unge-mærkede mindst fem år gamle ('young') er vist hver for sig.

	n	Pct. return	G_1	P
Females				
Adults, fledging	232	82.3	0.12	0.73
Adults, not fledging	231	83.5		
Young, fledging	292	71.9	1.15	0.28
Young, not fledging	361	75.6		
Males				
Adults, fledging	372	85.8	5.31	0.02
Adults, not fledging	352	79.3		
Young, fledging	108	80.6	0.31	0.58
Young, not fledging	148	77.7		

For older birds the number alive at the start of the considered period is not usually known, so the recovery rate cannot be calculated directly but must be estimated in some way. In the recovery analysis discussed in Appendix 2, annual estimates were found for three periods, 1959-1974 (0.082 ± 0.013 SE), 1969-1984 (0.067 ± 0.011 SE), and 1979-1994 (0.063 ± 0.009 SE). These values are only about half the size of the recovery rates for first-year birds, but the mortality of adults is also much lower than of first-years, so shooting appears to be at least as important a factor in adults as in young birds.

Life expectancy

With an annual survival of 0.75-0.80, adults of any age may expect a further life span of four to five years. If we want statistics on the life span of the geese, however, we have to limit the sample to cohorts with no known surviving members by the end of the study, or as it turns out, to birds born in the period 1959-1981. A total of 401 sexed birds from this period (258 females, 143 males) are known to have survived at least until the age of two years (Fig. 15). Decreasing numbers achieve higher ages, and the parameters of the fitted exponential curves correspond to an annual survival of 0.739 for females and 0.757 for males, which are similar, to the return rates discussed previously.

A constant survival of this magnitude corresponds to an additional life span of 3.83 years for females and 4.11 years for males. The observed means shown in the bottom graph of Fig. 15 are close to these values for birds achieving ages of up to 9-10 years, whereas observed additional years for older birds decrease steeply. This pattern is an effect of the limited life span of the birds, and of other deviations from the simple model of age-independent survival.

Only six birds (four females, two males) attained an age of more than 15 years. The oldest, the female #2191 reaching the exceptional age of 22 years, had an interesting career. Hatched in 1968, she spent the years to and including 1981 at Utterslev Mose where she reared 47 goslings. The following many years, from 1982 to 1989, she reared at least 25 goslings at Damhussøen about 4 km from Utterslev Mose, before she returned to her old breeding site and reared two young in 1990. The following winter she was found shot in Spain. Another female, #2331 hatched in 1969 and shot in Denmark in October 1985, also exemplifies that females will not always remain faithful to their place of birth. She stayed as a regular non-breeder at Utterslev Mose until 1973 and was seen occasionally even in 1974 and 1976, but was not heard of ever since until the message of her demise reached the Ringing Centre in Copenhagen.

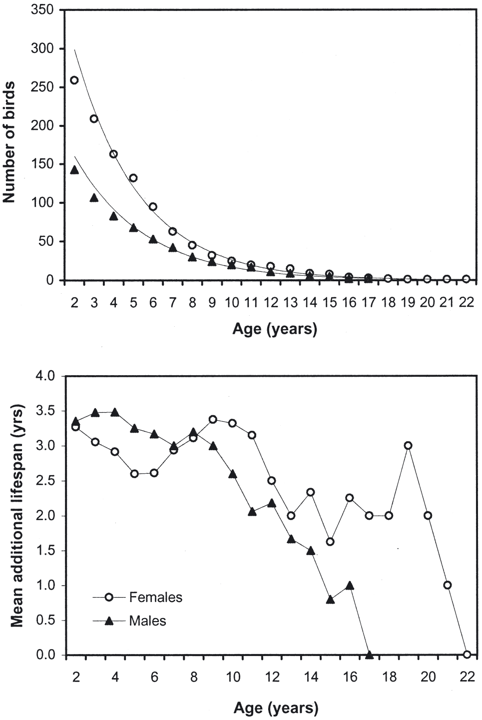
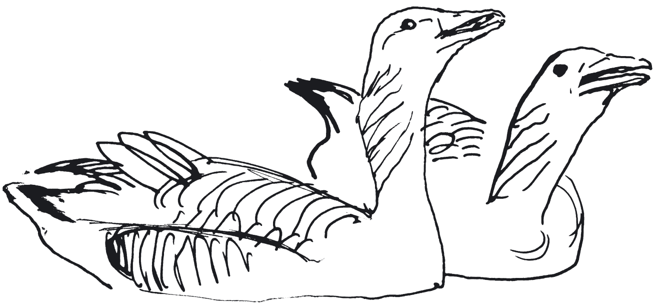


Fig. 15. Life span of sexed geese hatched 1959-1981 and attaining an age of two years or more. Top: number achieving at least the shown age, with fitted exponential curves added. Bottom: observed mean additional life span (length of life from present age onwards).
Livslængde for kønsbestemte gæs klækket 1959-1981, der opnåede en alder af mindst to år (hunner: åbne cirkler; hanner: fyldte trekanter). Øverst er vist antallet, der mindst opnåede den angivne alder. Nederst er vist den gennemsnitlige, resterende levetid for fugle med den angivne alder. I modeller med konstant dødelighed fås i det øverste tilfælde faldende eksponentialkurver som de indlagte; i nederste tilfælde ændres den resterende levetid ikke med alderen. Gæssene i Utterslev Mose afviger tydeligvis fra den simple model, bl.a. – og især – ved at levetiden er begrænset.



Reproduction

From adolescence to adulthood – becoming a breeder

Greylag Geese do not breed in their first spring, when almost one year old. They may, however, associate pairwise, although it may be questioned to which extent this should be considered as real pair formation. Of 98 2-year old mated females known to have been mated even in the previous year, 22 kept together with the previous mate and 22 had a new mate (the remaining 54 had an unringed mate in both yeas). Even in the second year the pair bond appears to be rather loose: of 332 females mated both when 2 and 3 years old, 64 stayed with the mate of the previous year and 55 associated with a new one. During the following years the proportion approached 2:1; of 1038 mated females ringed as goslings and aged four years or more, 382 stayed with the mate of the previous year and 179 had a new, while the corresponding figures for 527 mated females ringed as adults were 192 and 106. After the first few years, most cases of mate shift were caused by the disappearance and presumed death of the mate (see below).

The gradual incorporation of the young geese into the ranks of the breeders is illustrated in Fig. 16, with sample sizes shown in Fig. 17. There is some ambiguity as to the sample on which best to base frequency distributions of breeding status – e.g. fledglings or birds surviving to the age in question – but in order to make frequencies add up to 100% and so make mean ages well defined, the choice in Fig. 16 was the birds attaining the status category shown (all birds being mated at least once during their lifetime, etc.). So defined, the mean age for females of first mating was 1.90 ± 0.66 years, of first breeding attempt 3.31 ± 0.98 years, of first successful hatching 4.17 ± 1.60 years, and of first successful fledging 4.51 ± 1.80 years. For males the corresponding figures were 1.84 ± 0.66 years (mating), 3.51 ± 1.05 (breeding), 4.42 ± 2.01 (hatching), and 4.74 ± 2.08 (fledging). None of the age differences between sexes is statistically significant (t-test, $P = 0.16\text{-}0.46$), but for the age of first successful hatching the variance was greater in males than in females ($F_{47,161} = 1.58, P = 0.02$).

It appears from Fig. 16 that a small minority of the geese postpone breeding until a quite advanced age. Female # 7601 was born in 1983 and first bred (unsuccessfully) when five years old, and only managed to raise broods in the last two of her 10 years of living. Another female, # 7108 born in 1982, was mated each year from 1984 until last seen in 1990, but only bred during the last three years, each time without success. Male # 3349, born in 1976, first bred when six years old, but hatched no goslings until two years later; nevertheless, he managed to rear three broods within his 10-year life span.

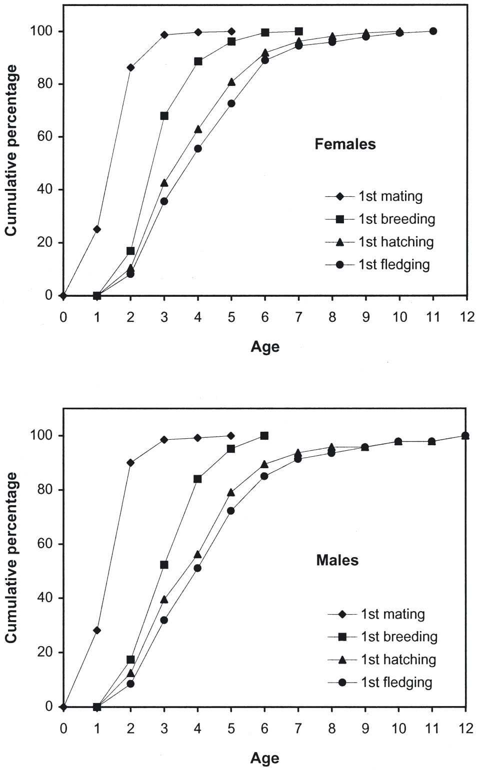


Fig. 16. Start of breeding of female and male Greylag Geese. Only regular Utterslev Mose birds born during 1959-1983 are included. The graphs show cumulated percentage of birds based on the total number in each category, i.e., all females (males) attaining mated status, etc. Sample sizes are given in Fig. 17 (total number of females that mated = 319 - 4 = 315, etc.).
Ynglestart for fugle født 1959-1983. Den kumulerede procentdel af fuglene, der første gang forsøgte at yngle ('1st breeding') i den angivne alder, og tilsvarende for første udparring ('1st mating'), første vellykkede klækning ('1st hatching'), og første gang kuldet overlevede og forblev sammen med forældrene til det var flyvefærdigt ('1st fledging') (n-værdier bag procenterne fremgår af Fig. 17).

Greylag Geese tend to pair with mates of similar age. During the study period there were 1296 pair-seasons where both female and male were ringed, but in many cases one or both pair members had been ringed as adults, leaving 494 pair-

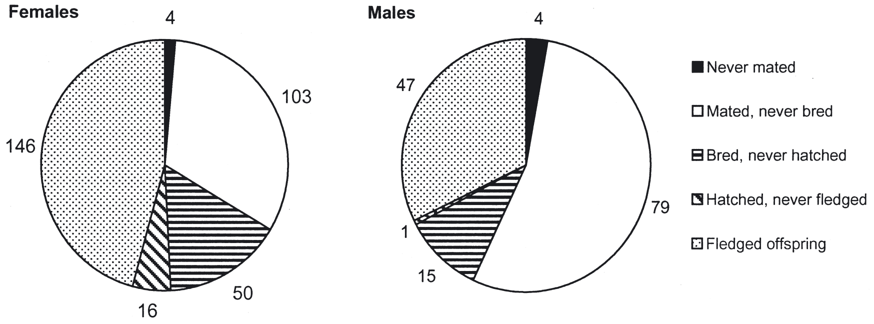


Fig. 17. Breeding status of regular UM geese born in 1959-1983 (same samples as in Fig. 16). n = 319 for females, n = 146 for males.
Ynglestatus for regelmæssige UM-gæs født 1959-1983 (samme som i Fig. 16).

seasons where the age of both sexes was known. The age of pair members was closely correlated (r = 0.799, P = 10^{-110}), and the mean age of females (4.10 years) was very similar to the mean age of males (4.17 years). If pairs with adult-ringed males were included, females had a mean age of 5.04 years (n = 923), and in the total sample of males the mean age was 4.55 years (n = 600). If only newly formed pairs were considered, so each pair contributed only once, the age of both sexes was known in 241 pairs out of a total of 631. Even here the correlation between female and male age was strong (r = 0.655, P = 10^{-30}). The mean age of pair members with known-age mates was 2.81 years for females and 3.06 for males (the difference not being statistically significant, t_{480} = 1.22, P = 0.22), while the mean age at pair formation for all 452 known-age females was 4.00 years, and for all 295 known-age males 3.43 years.

Breeding propensity

Even after their first breeding experience, Greylag Geese will not breed every year. Fig. 18 shows the proportion of birds of a given age that attempted to breed at Utterslev Mose. The entire sample of regular, sexed birds is included – since comparisons are made within age-classes, there is no reason to restrict the sample to birds born some time before the end of the study, as was necessary in connection with Fig. 16 and other cases, and for example the subsample of birds born in 1959-1983 (as in Fig. 16) gives graphs almost identical to those of Fig. 18. In both sexes the proportion in all three categories grows nearly linearly until the age of six years and then levels off. Almost all 2- and 3-year old birds are first-time breeders and most birds older than four years experienced breeders (cf. Fig.

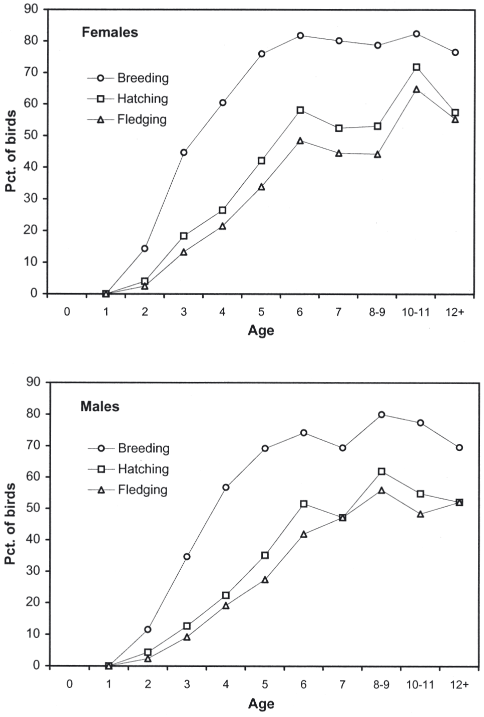


Fig. 18. Proportions within age-classes of females and males attempting breeding, hatching clutches and fledging young. For females, the maximum age was 18 years; sample sizes for the ten age-classes shown were, respectively, 669, 573, 430, 321, 242, 165, 101, 113, 57, and 47. For males, the maximum age was 17 years, and sample sizes were 296, 251, 173, 125, 91, 62, 36, 50, 31, and 23. Regular UM birds ringed as goslings 1959-1993.
Procentdelen af gæs inden for hver aldersklasse, som i gennemsnit forsøgte at yngle i et givet år ('breeding'), som klækkede et kuld ('hatching'), og som fik flyvefærdige unger ('fledging'). Øverst hunner, nederst hanner. Regelmæssige UM-fugle 1959-1983.

16), but even birds eight years old or more will only breed in about four years out of five (females 79%, males 77%, according to Fig. 18).

Another way of looking at this, also showing the very large variation among individual birds, is to compare the number of breeding years with the length of the entire life span, as done in Fig. 19 for regular UM females born 1959-1981. Potentially, a female may breed each year except one (the first) during its lifetime, but very few manage that. However, among the most long-lived birds, five remarkable females bred in more than ten years: females # 2473 and # 3390, born in 1972 and 1977, both bred during 11 seasons, hatching 10 and 9 clutches and fledging 9 and 8 broods, respectively. Female # 2427 from 1971 bred 12 times during her 15-year life span, hatched 8 clutches and fledged 6 broods. And females # 2959 (1976) and # 3387 (1977) both lived for 15 years, bred in 14, and hatched and fledged 11 and 5 broods, respectively.

Nest and fledging success

It appears from Fig. 18 that, as an average, a quarter to one third of the nests of experienced breeders fail, while nest success of younger birds is lower. Complete brood losses also occur, but here an age effect is less apparent. As will be seen in the next section, brood losses appear to be caused primarily by another pair adopting the brood and not as much by mortality.

The frequency of brood loss, and especially of nest failure, vary from year to year (Fig. 20), but without any trend (hatching success r = -0.16, P = 0.38; fledging success r = 0.07, P = 0.70) and not in step with each other – on the contrary, a negative correlation is suggested but not statistically significant (r = -0.24, P = 0.20). The problems the geese saw in the early 1980s, thought to be caused by conditions in the wintering area, is reflected in a very poor nesting success in 1980-1981, which could be a result of females returning in spring with insufficient nutrient reserves. The rather low nest success towards the end of the study period could be caused by a high proportion of the females being rather young – the average nest success in Fig. 20 (1964-1994) is 59.9%, while the corresponding figure for females aged 6 years or more is 71.7%, and for females ringed as adults 76.2%. Mean fledging success in Fig. 20 is 83.8%, giving a total breeding success of 50.2% in 1435 breeding attempts; for females 6+ years old, mean fledging success is 85.1% and total success 61.0% (403 breeding attempts), and for females ringed as adults the figures are 90.1% and 68.6% (370).

Female # 3390 (left) was born in 1977 and mated to male # 4316 (right) from 1979 to 1990, her last season. He was ringed as an adult in 1979 and was still alive at the end of the study in 1994. Together they fledged 36 goslings. Utterslev Mose, April 1981.

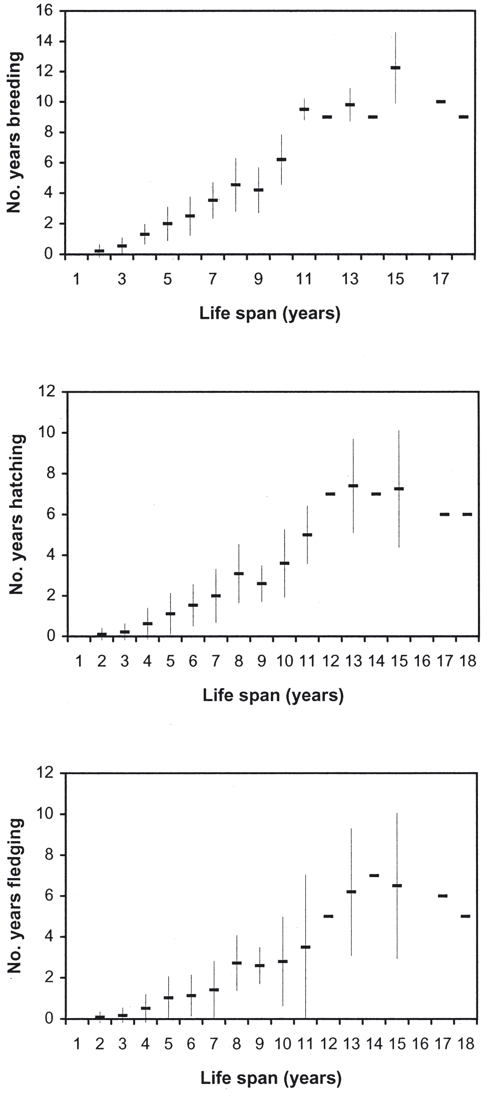


Fig. 19. Relationship between total life span and mean number of years in which female geese attempted to breed, hatched clutches, or fledged young. Error bars show 1 SD. Regular UM birds born 1959-1981 and living for at least two years (n = 241 for total sample; for the shown classes (life span 2-18 years) n = 50, 46, 29, 35, 28, 17, 11, 5, 5, 2, 1, 5, 1, 4, 0, 1,1).

Gennemsnit og standardafvigelse for antal år i hvilke hunner forsøgte at yngle (øverst), klækkede et kuld (midten), og fik flyvefærdige unger (nederst), sammenholdt med levetiden (x-aksen). Regelmæssige UM-gæs født 1959-1981 og fortsat live ved alderen to år.

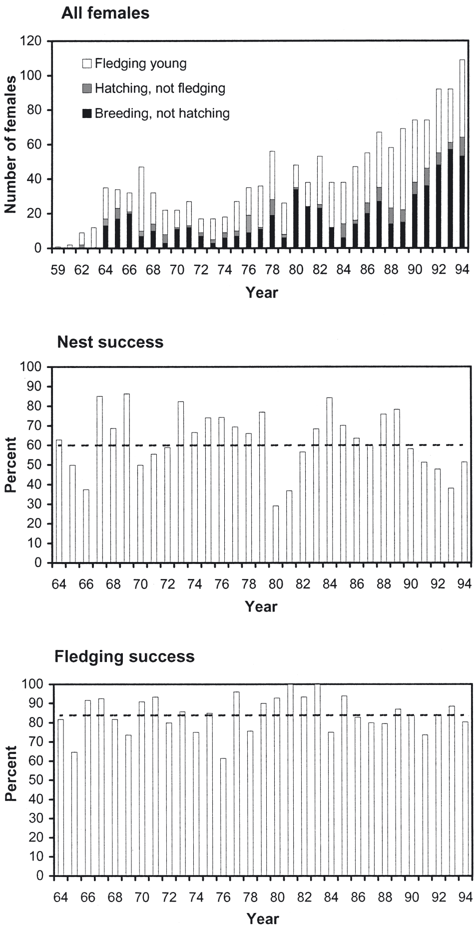


Fig. 20. Breeding attempts by ringed females throughout the study period. Entire sample, including both birds ringed as goslings and as adults. Nest success is the proportion of nests hatching at least one gosling, and fledging success is the proportion of broods that stayed together with the female and from which at least one gosling fledged.

Øverst: antallet af ringmærkede hunner, der hvert år lagde æg, men mistede dem før klækningen ('breeding'), som fik gæslinger, men mistede dem før de var flyvefærdige ('hatching'), eller som fik flyvefærdige unger ('fledging'). Midten: den årlige redesucces (procentdel af kuld hvorfra mindst en unge klækkedes). Nederst: den årlige kuldsucces (procentdel af ungekuld hvor mindst en unge blev flyvefærdig).

Brood size and survival of goslings

In the absence of direct observations of female geese leaving the nest with newly hatched goslings, the exact initial size of broods cannot be stated, so instead the size when first seen is used as an approximation. The mean initial size of all broods with known female parents recorded at Utterslev Mose was 5.12 ± 3.05 SD (n = 858). There was some variation between years but no overall time trend (Fig. 21).

However, to summarise brood size by a single number is a dubious practice. Apart from the annual variation, brood size is usually found to depend on parent age and/or experience, laying date, and other factors. For the UM geese an effect of the age/experience of the mother is apparent (Table 12; for statistics, see below), and an effect of laying date is suggested (early broods 5.11 ± 2.52, late broods 4.55 ± 2.48, $t_{827} = 3.19$, $P = 0.0015$). The latter, however, appears mainly to be a consequence of the former, since young females lay late and have small clutches. Within age-classes, the effect of laying date is slight and not always in the expected direction.

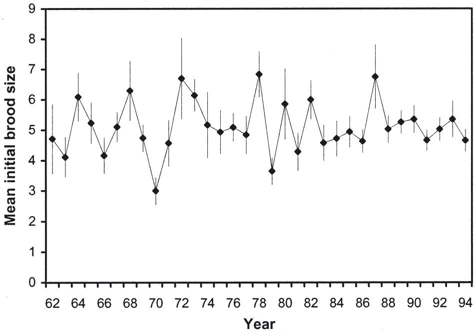


Fig. 21. Initial size of broods (mean ± SE) of ringed female Greylag Geese in Utterslev Mose, 1962-1994. There is no trend (r = 0.053, P = 0.77).
Den årlige gennemsnitsstørrelse af ungekuldene kort efter klækningen. Der er ingen signifikant tendens.

Another concern is to which extent the observed initial brood size reflects the true number of goslings parented by the apparent mother. No correction for intra-specific nest parasitism can be made in the present data, but the potentially more

Table 12. Initial brood size vs age of female parent. Brood size of females ringed as adults is shown separately (Ad.). Only broods with 12 or fewer goslings are included (see text). Early broods hatched before the mean hatching date of the year, late broods hatched later. In addition to the whole sample, broods that were not subsequently enlarged by adopted goslings are shown separately.
Størrelsen af gæslingekuld i Utterslev Mose når de først sås et par dage efter klækningen (1962-1994). Ud over det fulde materiale ('all broods') er separat vist de kuld, der ikke senere modtog adopterede gæslinger ('with no adoption'). Kuldene er opdelt efter moderens alder (kuld af adult-mærkede mødre vist separat ('ad.')), og yderligere på dem set før ('early') og dem set efter ('late') gennemssnitsdatoen for det pågældende år.

Age of	Early broods			Late broods			All broods		
female	N	Mean	SD	N	Mean	SD	N	Mean	SD
All broods									
2	3	9.33	2.52	20	3.45	1.54	23	4.22	2.59
3	19	3.95	2.39	58	4.19	2.09	77	4.13	2.15
4	27	5.37	1.92	57	3.96	2.20	84	4.42	2.20
5+	189	4.84	2.39	189	4.53	2.44	378	4.68	2.42
Total	238	4.88	2.40	324	4.30	2.30	562	4.55	2.36
Ad.	122	5.56	2.68	145	5.12	2.75	267	5.32	2.72
With no adoption									
2	2	8.00	1.41	17	3.35	1.50	19	3.84	2.06
3	15	3.27	2.09	50	3.98	2.06	65	3.82	2.07
4	18	5.00	1.75	46	3.74	2.22	64	4.09	2.16
5+	125	4.50	2.28	155	4.28	2.15	280	4.38	2.21
Total	160	4.49	2.26	268	4.07	2.12	428	4.23	2.18
Ad.	75	5.33	2.37	103	4.27	2.19	178	4.72	2.32

Photo: Vibeke Tofte.

serious source of error represented by early brood amalgamation or adoption of partial broods may be addressed. Adoption is treated in detail in the next section, and in the present context it suffices to mention that broods of more than 12 goslings are strongly suggestive of adoption, and that some broods exceeded this size already when first seen. In order to estimate true brood size, these large broods should hence be disregarded (as were done in Table 12), but that may not solve the problem since other broods, of more likely size, may also have been enlarged before they were discovered. That this possibility should not be ignored appears from Table 12, where in addition to the entire sample, broods not receiving adopted goslings at some later time in the brood-rearing period are treated separately. Mean initial brood size is generally smaller in these broods than in the total sample, and therefore smaller than in broods that did receive adopted goslings. A likely explanation is that socially dominant pairs both tend to produce large broods and are particularly liable to adopt other goslings, but the possibility remains that some broods had been enlarged before they were discovered, and that these broods are mainly to be found among those later enlarged (further), the idea being that adopting pairs will often do it repeatedly.

Even if this suggestion is correct, there is no guarantee that the sample of broods apparently not involved in adoption after they were first seen had not already been enlarged, although it would appear more likely that they were reduced – the adopted goslings, after all, must come from somewhere. There is some indication, however, that goslings adopted early often originate in broods never seen together with their parents (see below). In conclusion, both samples in Table 12 may be biased, but in opposite directions: brood size in the 'no adoption' sample biased downwards (owing to an over-representation of subdominant pairs), brood size in the 'adoption' sample biased upwards (owing to an over-representation of dominant pairs and to the inclusion of some adopted goslings in the "initial" broods).

Based on the 'no adoption' sample in Table 12, females of age 2 and 3 years produced slightly fewer goslings than older females, 3.82 per brood against 4.33. The difference between females 2-3 years old and females older than 4 years is significant (t_{362} = 2.03, P = 0.043), largely corresponding to the difference between first-time breeders and experienced breeders (only five 3-year old females had also produced a brood the previous year, one of them in the 'adoption' sample). There also seems to be a difference between older females ringed as goslings and those ringed as adults, the latter producing 0.34 goslings more per brood than the former, but the difference is not statistically significant ($t_{456} = 1.58$, $P = 0.12$).

Individual goslings could not be followed before they were ringed, so no direct information is available on survival through the brood-rearing period. By comparing initial and final brood sizes summed over pairs, however, it appears to be very high. Fig. 22 shows the apparent survival of goslings calculated as added final brood sizes divided by added initial brood sizes for each year during 1962-1994, for all pairs with at least one ringed member. Female parents ringed as goslings are shown separately from those ringed as adults (in the relatively few cases where only the male was ringed, the assignment to group was based on the ringing age of the male). Overall, there were 4752 goslings in the beginning of the brood-rearing period and 4303 goslings towards the end, giving a mean apparent survival of 90.6 %. For parents ringed as goslings, the corresponding figures were 2966 and 2561 (86.3 %), and for parents ringed as adults they were 1786 and 1742 (97.5%).

The difference between the two groups probably reflects a poor performance of young parents in the group ringed as goslings, both in terms of securing the survival of their offspring and of keeping them from being taken over by another pair. A net movement of goslings from parents ringed as goslings to parents ringed as adults is suggested by the inverse, although not statistically significant

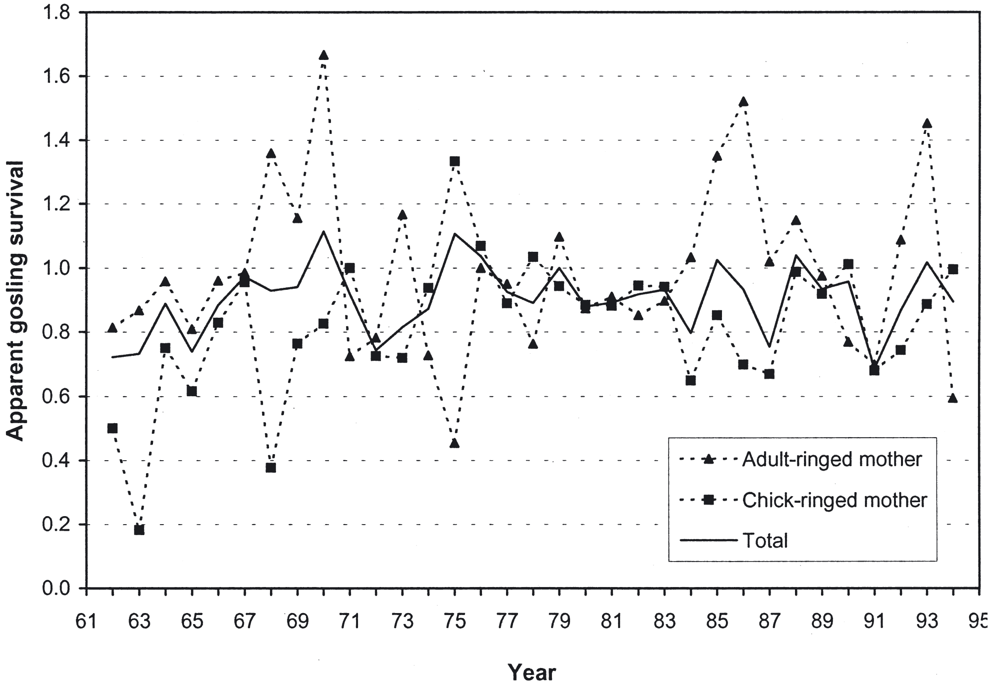


Fig. 22. Apparent survival of goslings in Utterslev Mose, 1962-1994. Survival is estimated as the total number of goslings of marked parents (or foster parents) present at the end of the fledging period divided by the total number of newly hatched goslings of marked pairs. In addition to the total sample, apparent survival is shown separately for offspring of females ringed as goslings and females ringed as adults (or similarly for males in the few cases where only the male was ringed). A few broods with unknown initial size are excluded. Values exceeding 100% are discussed in the text.
Tilsyneladende årlig ungeoverlevelse: det totale antal gæslinger med ringmærkede forældre (eller adoptivforældre) i slutningen af sæsonen i forhold til det totale antal nyklækkede gæslinger af mærkede par. Ud over totalen af gæslinger (fuldt optrukket streg) er stiplet vist tilsvarende kurver alene for par, hvor hunnen var mærket som unge (firkanter), og for par hvor hunnen var mærket som adult (trekanter); de få kuld, hvor kun hannen var ringmærket, er i stedet grupperet efter hannens alder ved mærkning. Fordi gæslinger kunne adopteres mellem disse grupper, er der ikke noget naturstridigt i en tilsyneladende overlevelse på over 100%. Noget tilsvarende gælder totalen, fordi der altid var nogle få par, hvor ingen af magerne var mærkede. Alligevel tyder mønstret på, at kuld undertiden blev adopteret af andre par før de var registreret sammen med forældrene.

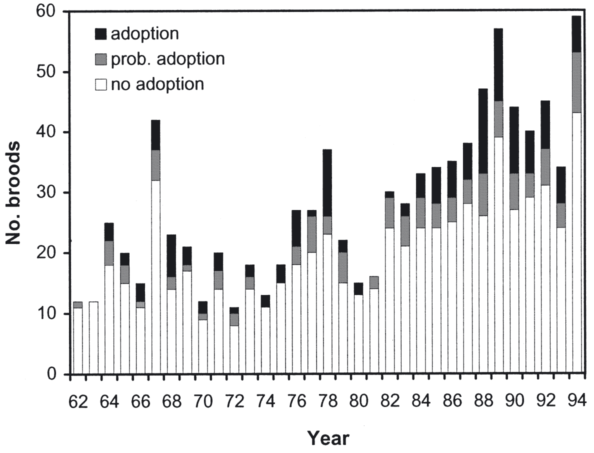
relationship (r = -0.280, P = 0.12) between apparent gosling survival in the two groups. However, this cannot explain that the apparent survival for both groups combined exceeded 100% in six of the 33 years, and the generally high survival of goslings produced by parents ringed as goslings likewise indicates that net loss to geese ringed as adults was not very marked. Unringed pairs could have been a source of adopted goslings for one or both groups of ringed geese, but unringed pairs were few, and why they should have been particularly prone to loose goslings to other pairs is difficult to understand. There remains the possibility that in some years a few pairs lost their brood to another pair so early that the brood was never seen together with the parents, in which case the apparent survival for the total ringed sample (90.6%) overestimates true survival, but probably not very much – survival of goslings during the brood-rearing period certainly appears to be high in the Greylag Goose population of Utterslev Mose.

The possibility that some pairs lost their brood before it could be recorded also implies that nest success, discussed in the previous section, could be slightly underestimated.

Adoption of goslings

Persson (2002) argued that, although a single female may lay as much as 12 eggs, incubation of more than 10 eggs appears to be difficult and normally only partially successful. Broods of 11 or 12 goslings, hence, should be suggestive of adoption, and larger broods should definitely contain adopted goslings..

In the present analysis, pairs hatching young were assigned an adoption-score dependent of



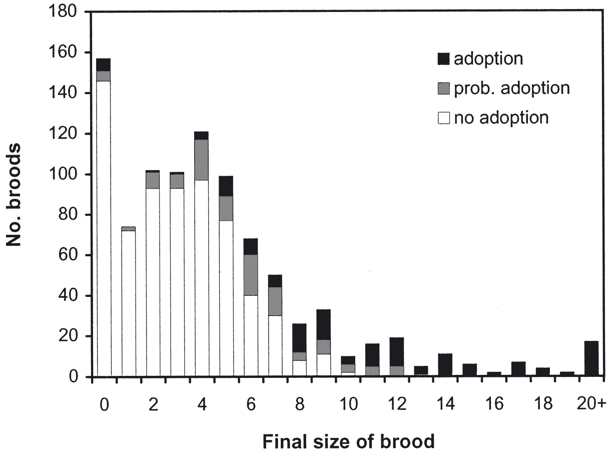


Fig. 23. Adoption of goslings in 930 broods of Greylag Geese in Utterslev Mose. In 669 broods no indication of adoption was recorded, in 114 the evidence was not entirely conclusive, while in 147 adoption was established with certainty. Top: number of known broods per year. Bottom: number of known broods according to adoption status and final brood size.

Antal kuld med (sort) og uden (hvidt) adopterede gæslinger, samt kuld hvor adoption sandsynligvis forekom, men hvor en vis usikkerhed om det stod tilbage (gråt). Øverst: kuld fordelt på år. Nederst: kuld fordelt efter størrelsen sidst på sæsonen. Kuldene blev fulgt hele ungetiden, så kuld med adoption kunne godt ende med at være meget små. En kuldstørrelse på nul angiver, at alle unger døde eller blev overtaget af et andet par.

Table 13. Mean age of female or male parent in broods where adoption did or did not occur. The age of the other parent was ignored, and most often unknown, but generally the geese tended to pair with mates of similar age.
Gennemsnitsalder af ynglende Grågåse-hunner ('females') og -hanner ('males'), der a) ikke adopterede fremmede unger i ungeføringsperioden, b) som tilsyneladende gjorde det, og c) som med sikkerhed gjorde det. Tilsyneladende er gennemsnitsalderen højere hos de forældrefugle, der adopterer fremmede gæslinger, men tendensen er kun signifikant hos hannerne.

	Mean	SD	n	test	t	df	P
Females							
a: No adoption	5.88	2.82	427	a vs b	0.953	494	0.34
b: Prob. adoption	6.23	2.98	69	b vs c	0.307	149	0.76
c: Adoption	6.37	2.38	82	a vs c	1.461	507	0.14
Total	5.99	2.78	578	a vs b+c	1.619	576	0.11
Males							
a: No adoption	6.02	2.91	152	a vs b	2.405	180	0.02
b: Prob. adoption	7.47	3.48	30	b vs c	0.187	60	0.85
c: Adoption	7.31	2.99	32	a vs c	2.272	182	0.02
Total	6.42	3.06	214	a vs b+c	3.025	212	0.003

how strongly adoption, at any time during the brood-rearing period, was indicated. The broods were recorded repeatedly, so indicators of adoption were not limited to the initial and final size of broods. The adoption-score had four levels: score = 0, no sign of adoption; score = 1, adoption probable, but not certain (brood 11-12 goslings, and/or increasing by 1-2, at any stage); score = 2, certain adoption, but involving a moderate number of goslings only (brood 13-17, and/or increasing by 3-5); and score = 3, certain and extensive adoption (brood ≥18, and/or increasing by ≥6). Increases by 1-2 goslings were considered probable indicators only to allow for occasional miscounts or partially hidden broods; they accounted for all but 20 of the 114 broods assigned an adoption score of 1.

Adoption by these criteria occurred throughout the study period, with some variation between years (Fig. 23). If the ambiguous adoption-score 1 is pooled with scores 2 and 3, the overall percentage of broods containing adopted goslings at some stage during the brood-rearing period is 28.1%, which may be considered an upper limit; if it is pooled with score 0, the percentage is 15.8%, and if it is disregarded the percentage is 18.0%. In all three cases there is a positive tendency over time (r = 0.27-0.42), but it is significant only if score 1 is pooled with scores 2 and 3 (P = 0.02); in the two other cases significance levels are P = 0.09 and P = 0.12, respectively. It should be noted, that indications are found below that adoption was indeed involved in broods assigned a score of 1.

Not surprising, adoption and final brood size are closely interrelated although, as defined, adoption may occur in broods of modest or low final size, even zero (Fig. 23).

Even young parents may adopt goslings – in one certain case the female was only two years old, but the male had recently been ringed as an adult and was probably some years older. Since a connection between adoption and dominance status would seem natural, however, it might be assumed that older parents are more likely to adopt goslings than younger parents. To elucidate the role of parent age and adoption is not that easy, however, because many breeders were either unringed or ringed as adults and hence of unknown age. There were 578 broods where the female was ringed as gosling, and 214 broods where the male was. But in only 121 broods were both parents of known age, and only 14 of these certainly contained adopted goslings (score 2-3), while 91 had a score of 0.

The mean age of female and male parents of broods grouped according to adoption status is shown in Table 13. For females, mean age grew with adoption status, but none of the differences were statistically significant. Males involved in adoption, however, were significantly older than males parenting broods with no indication of adoption. This difference was seen even where adoption was considered probable only, suggesting that the majority of these broods had indeed experienced adoption. Also in females, despite the non-significant differences, the mean age of probable adopters was closer to the mean age of certain adopters than to those not adopting.

In spite of the noise in the data caused by the unknown age of the male parent, an alternative approach appears to confirm a relationship between age and frequency of adoption in the female sample. If sequentially excluding broods with the youngest female parents and comparing frequencies of three adoption-classes (score 2 and 3 combined), a difference between females ringed as young and females ringed as adults was still suggested when broods of 4-year old females were excluded (G_2 = 5.03, P = 0.08), but not when 5-year old females were excluded too (G_2 = 2.00, P = 0.37). A similar test in males gave no difference between any subgroup of birds ringed as goslings and those ringed as adults, probably due to the low number of birds of known age in this sample.

A few pairs have been surprisingly precocious in terms of adoption, despite the generally infrequent occurrence in young pairs. In 1990, a pair in which both members were three years old hatched six goslings and was later seen with 12, before ending up with 11 at fledging. Another young pair, the female aged three years and the male four, did even better in 1993 when starting with 9 goslings and ending up with 14 after having had 16 at some point during the brood-rearing period. There have also been two pairs, both of two 4-year old birds, which went, respectively, from four to eight goslings, and from five to ten and back to five. However, the most spectacular examples of adoption seem to involve fairly old parents. Seven broods ended with 25 or more goslings. In none of these broods were both parents of known age, and in one both parents had been ringed as adults in the previous year. In three pairs the female was 6, 10, and 12 years old, respectively, while in three other pairs the male was 8, 8, and 11 years. The largest brood had 39 goslings and was accompanied by the 12-year old female together with a male ringed as an adult three years earlier.

Factors affecting breeding output and return rates of offspring

Parent survival

Initially it may be of interest to consider the survival of goslings that lost their parents before the following spring. Since goslings stay together with their parents for all or most of this period, the loss of one or both could be expected to have grave consequences, especially if it happened early.

Return rates of fledged goslings are shown in Table 14, grouped according the survival of the parents. Disregarding the four groups in which the fate of one parent was unknown, there was a clear heterogeneity between groups, with lower return rates of goslings losing one parent and, especially, both parents, compared with goslings whose parents survived. However, some did survive, even after losing both parents. It also looks as if gosling survival depends more strongly on the survival of the father than of the mother, the difference being significant in the sample of all goslings (G_1 = 5.27, P = 0.022 (P = 0.027 with Yates' correction)), but not in the sample of female goslings (G_1 = 0.65, P = 0.42). Nevertheless, in a large brood which kept its mother but lost its father already in late May (before fledging), 8 of 15 goslings (5 of 8 females) returned.

The time of death of parents is known only for the minority that was recovered, and no relationship between time of parent death and return of goslings is apparent, probably because the sample is small, and because the other parent often survived, at least for some time. In only four broods were both parents recovered. In one, of which the parents were both shot in September, one of the two goslings (both female) returned, while in two other broods in which the parents were both shot in November-December, 3 of 8 goslings (2 of 4 females) returned. In the last, where male and female were shot in August and November, respectively, none of the four goslings is known to have survived.

Change of mate

There were 1022 cases in the total sample where it could be established whether the mate of a female was the same as in the previous season, or had been replaced (Table 15). These cases involve ringed females mated to ringed males, or to unringed males if the male in the other of the two consecutive seasons was ringed.

Table 14. Apparent survival (return rate) of goslings of parents that survived to the following year, and of parents that were never seen in later seasons. Broods reared 1966-1993. f (m) indicates loss of female (male) parent, f? (m?) the possible loss of unringed female (male) parent. Disregarding the four groups in which the fate of one parent was unknown, there was a clear heterogeneity between groups (all goslings: $G_3 = 43.3$, $P = 2\cdot10^{-9}$; female goslings: $G_3 = 21.0$, $P = 0.0001$).

Tilsyneladende overlevelse til det følgende år ('pct. returned') af UM gæslinger afhængigt af forældrenes overlevelse. I mange par var hunnen (f?) eller hannen (m?) umærket, hvorfor det ikke vides om den overlevede. Derudover viser søjlerne overlevelsen af gæslinger fra par, hvor ingen ('none') af forældrene døde inden næste forår, hvor hunnen gjorde (f), hvor hannen gjorde (m), og hvor både hunnen og hannen gjorde ('both'). Foruden det fulde materiale er separat vist de gæslinger, som blev bestemt til hunner.

	Parent lost								Total
	none	f?	m?	f	m	f, m?	m, f?	both	
All goslings									
Ringed	1183	150	44	304	273	102	9	165	2230
Returned	635	61	27	140	100	40	2	56	1061
Pct returned	53.7	40.7	61.4	46.1	36.6	39.2	22.2	33.9	47.6
Female goslings									
Ringed	577	62	22	153	124	48	3	80	1069
Returned	358	33	15	79	58	23	0	33	599
Pct returned	62.0	53.2	68.2	51.6	46.8	47.9	0.0	41.3	56.0

Table 15. Paired female geese. Number of seasons, grouped according to breeding status and identity of mate (i.e., whether it was the same as in the previous season or not). Cases where the status of the mate could not be established, or where the female had not been paired in the previous season, are omitted. Overall, similar proportions of females ringed as adults and females ringed as young had new mates ($G_1 = 0.004$, $P = 0.95$). The relationship between mate shift and breeding success is tested in Table 16.

Udparrede hunner, der havde været udparrede også i det foregående år: antal sæsoner i hvilke magen var den samme ('previous mate'), og i hvilke magen var ny ('new mate'). Hunner mærket som adulte og unger er vist separat. Ynglestatus: (not) breeding = (ikke) ynglende; (not) hatching = ynglende, fik (ikke) gæslinger; (not) fledging = klækkede ægkuld, fik (ikke) flyvefærdige gæslinger. Samlet var hyppigheden af mageskift den samme for de adult- og de ungemærkede ($G_1 = 0,004$, $P = 0,95$). Betydningen af mageskift for ynglesuccesen undersøges i Tabel 16.

	Ringed as adults		Ringed as young	
	Previous mate	New mate	Previous mate	New mate
Breeding	157	64	356	155
Not breeding	35	42	112	101
Hatching	117	42	228	83
Not hatching	40	22	128	72
Fledging	104	34	208	64
Not fledging	13	8	20	19
All pairs	192	106	468	256

Since the females ringed as goslings include young birds, and since even some differences between older geese ringed as goslings and geese ringed as adults have been suggested previously, the two groups are treated separately in Table 15. It appears that there is no difference in frequency of mate shift between the two groups, but that the nest success of females ringed as goslings is less than of females ringed as adults. The data are analysed in more detail in Table 16, in terms of the in-

Table 16. Tests of significance of variation in breeding status or breeding success in Table 15.
Test af tallene i Tabel 15. Mageskift har en klar effekt på ynglestatus i alle stadier: om ynglen påbegyndes, om et kuld klækkes, og om ungerne overlever og bliver sammen med forældrene; men kun i det første tilfælde er der en signifikant effekt hos de adult-mærkede hunner, i de øvrige synes effekten alene at skyldes de unge-mærkede hunner. Den eneste signifikante forskel herudover er, at forholdsvis flere unge-mærkede end adult-mærkede hunner mistede eller opgav deres æg, uanset om magen var ny.

Source of variation between groups	G	df	P
Breeding/not breeding			
Age at ringing	1.35	1	0.246
Mate status	33.37	1	$8\cdot10^{-9}$
Residual (interaction)	1.29	1	0.257
Total	36.00	3	$7\cdot10^{-8}$
Adults tested separately	15.84	1	$7\cdot10^{-5}$
Young tested separately	18.81	1	$1\cdot10^{-5}$
Hatching/not hatching			
Age at ringing	8.36	1	0.004
Mate status	6.77	1	0.009
Residual (interaction)	0	1	1.000
Total	15.13	3	0.002
Adults tested separately	1.74	1	0.187
Young tested separately	4.95	1	0.026
Fledging/not fledging			
Age at ringing	0.04	1	0.838
Mate status	10.91	1	0.001
Residual (interaction)	0.68	1	0.408
Total	11.63	3	0.009
Adults tested separately	1.59	1	0.207
Young tested separately	10.00	1	0.002

Table 17. Paired females having new mates: cause of remating. The tests compare the frequency distribution of each of the two young-ringed samples with the adult-ringed sample.
Adult- og unge-mærkede hunner med ny mage: tilfælde hvor magen aldrig siden er set og formodes død ('by death'), og tilfælde hvor magen stadig var i live ('by divorce'). Ud over den fulde stikprøve af unge-mærkede hunner er separat vist de tilsvarende data alene for de hunner, der var mindst fem år gamle. Testen viser, at "skilsmisser" forekommer hyppigere hos de unge-mærkede hunner end hos de adult-mærkede, men at forskellen forsvinder når de yngste årgange sorteres fra.

Ringed as	New mate		G_1	P
	by death	by divorce		
Adults	51	22	–	–
Young	87	69	4.21	0.040
do. >4 years	56	33	0.87	0.352

fluence of age at ringing and mate status (previous or new) on breeding performance. Again it appears that the main effect of age at ringing is on the nest success (hatching success), and that this is caused by the presence of young breeders in the sample of females ringed as goslings is confirmed by the fact that the significance disappears when females younger than 5 years are excluded from the sample (P = 0.34). A more unexpected result of excluding the young females is that the effect of age at ringing on whether a female will breed or not becomes significant (P = 0.002), and that females ringed as adults are *less* likely to breed than those ringed as young. This means that the insignificant result in Table 16 (P = 0.246) is caused by a heterogeneity in the young-ringed sample: young birds less, and older birds more likely to breed than adult-ringed females, the two tendencies more or less cancelling each other in the full sample.

That mate shift has a marked effect on breeding performance is clear from Table 16. Mate shift appears mainly to affect the likelihood that a female attempts to breed, and in adult-ringed females the effect on hatching and fledging success is not significant. For young-ringed females the significant effect on likelihood of breeding persists after exclusion of birds less than 5 years old, but at a far weaker level (P = 0.038), and the effect on hatching success becomes insignificant (P = 0.075), indicating that mate shift affects young breeders more strongly than older breeders. The effect on fledging success, however, remains significant (P = 0.008). Fledging success, however, is not so much a component of breeding success as a measure of the pairs' ability to keep their goslings from being taken over by other pairs.

Females pairing for the first time in their life were not considered above. There was a total of 634 such cases, of which 537 pairs abstained from breeding, 63 nested but failed to hatch a clutch, 13 hatched a brood but lost it, and 21 fledged goslings. This is a much poorer performance than seen in the other newly formed pairs discussed above. A comparison with other young-ringed females with new mates gives $G_1 = 174.75$, $P = 7\cdot10^{-40}$ (breeding/not breed-

Table 18. Paired females ringed as adults, or as young and at least five years old, and having new mates: frequencies according to breeding status and cause of remating, and test of significance of source of variation. Only breeders are considered in the lower part.

Hunner med ny mage: sammenhæng mellem årsag til mageskiftet (død, skilsmisse) og ynglesucces. Af de unge-mærkede hunner betragtes kun dem, der ved tilfældet var mindst fem år gamle. Se også Tabel 15-17. Mht. påbegyndelse af ynglen (tabellens øverste halvdel) viser testen, at adult-mærkede hunner er særlig tilbøjelige til at afstå fra ynglen efter mageskift, især efter skilsmisse, sammenlignet med unge-mærkede. Mht. klækning af et kuld (nederste halvdel) ses en sådan forskel ikke umiddelbart, men det signifikante 'interaction' led viser, at de to grupper alligevel reagerer forskelligt: samlet er der ikke den store forskel på hvor stor en andel, der mister/opgiver æggene, men betydningen af død og skilsmisse er forskellig hos de to grupper.

	Adults: New mate		Young: New mate	
	by death	by divorce	by death	by divorce
Breeding	35	10	46	26
Not breeding	16	12	10	7

	G	df	P
Age at ringing	7.42	1	0.006
Cause of remating	1.86	1	0.172
Residual (interaction)	1.72	1	0.189
Total	11.01	3	0.012

	Adults: New mate		Young: New mate	
	by death	by divorce	by death	by divorce
Hatching	27	4	27	17
Not hatching	8	6	19	9

	G	df	P
Age at ringing	0.73	1	0.391
Cause of remating	0.74	1	0.388
Residual (interaction)	4.28	1	0.039
Total	5.76	3	0.124

ing), $G_1 = 8.30$, $P = 0.004$ (hatching/not hatching), and $G_1 = 2.76$, $P = 0.10$ (fledging/not fledging). If adult-ringed females with new mates are included, the difference becomes even more marked.

Females with new mates hatched smaller broods (4.78 ± 2.83 SD, n = 122) than females breeding with their mate from the previous season (5.33 ± 3.10 SD, n = 343), but the difference was not statistically significant ($t_{463} = 1.72$, $P = 0.09$). The few females paired for the first time that hatched goslings had even smaller broods (3.79 ± 3.19 SD, n = 34), but, probably owing to the small sample size, the comparison with other females having a new mate was not significant ($t_{154} = 1.74$, $P = 0.08$). Old pairs were also more prone to adopt goslings than newly formed pairs (129 of 343 old pairs vs 23 of 122 new pairs, $G_1 = 15.38$, $P = 9 \cdot 10^{-5}$), and the same held true if the dubious adoption-class 1 was disregarded (74 of 288 vs 13 of 112, $G_1 = 10.33$, $P = 0.0013$).

Finally, one might consider the cause of mate shifts. If we term cases where the female's former mate is known to be alive as divorce, and consider all former mates never seen again as being dead, there were 91 divorces among 229 cases where a female remated with a new mate (Table 17). Divorce is more common among females ringed as young, but if females younger than 5 years are excluded this difference is no longer statistically significant. A comparison of breeding status between widowed females and females acquiring a new mate after a divorce (Table 18) shows a significant age-at-ringing effect that was mentioned already in connection with Table 16: for some reason, females ringed as adults are more likely to abstain from breeding than females ringed as goslings (but at least five years old). For the females that did breed, there was no apparent difference in hatching success (or in brood size: death 4.83 ± 2.85, n = 53; divorce 4.90 ± 2.61, n = 21; P = 0.76) be-

Table 19. Breeding performance of female Greylag Geese in the last season before remating and the first season with the new mate. In all cases, the female had been paired with the previous mate for at least two seasons.
Ynglestatus (procentdel hhv. af ynglende fugle og af fugle med unger) samt kuldstørrelse før og efter mageskift hos hunner mærket som adulte og unger (jf. Tabel 17-18). Før ('before') henviser til det sidste år med den gamle mage, efter ('after') til det følgende år, det første med den nye mage. I alle tilfældene havde hunnen været sammen med den gamle mage i mindst to år i træk.

Cause of remating	Females	Pct. breeding		Breeding females	Pct. hatching		Goslings/hatching pair	
		Before	After		Before	After	Before	After
Ringed as young [1]								
Death	41	73	73	30	53	53	6.0	4.8
Divorce	18	89	72	13	85	77	4.3	4.5
Ringed as adults								
Death	20	90	75	15	73	80	4.3	4.3
Divorce	15	73	53	8	50	38	6.3	4.3

[1] only birds at least five years old included

tween the two groups, and neither did the cause of remating appear to affect breeding status or hatching success. However, there was a significant interaction in the test of hatching success, suggesting that females ringed as adults and young, respectively, responded differently to divorce and/or death of mate. And although the numbers are small, inspection of the frequencies do in fact suggest that the adult-ringed females responded strongly to being divorced, but rather weakly to being widowed, compared to females ringed as goslings. A similar strong response to being divorced is also suggested when looking at the breeding status, but there it did not manifest itself in the test, being swamped by the generally high frequency of non-breeding among females ringed as adults.

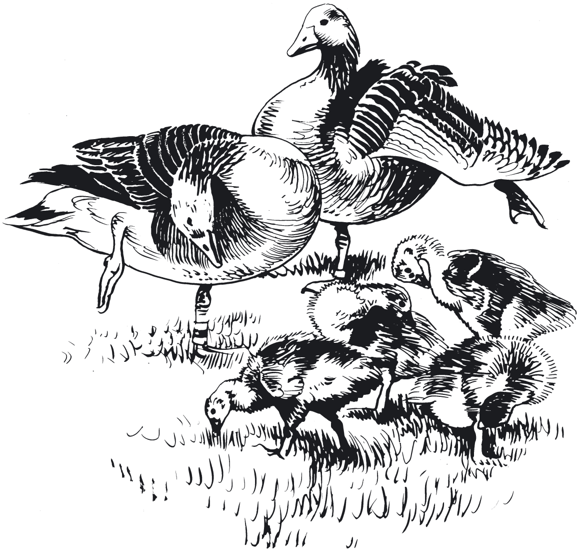
Properly, the comparisons above should be made between the same females before and after mate shift, and where the previous mate had not also been new. Unfortunately, these restrictions reduce the size of the available samples considerably. When applying the tests of the upper part of Table 18 (breeding vs not breeding) on this restricted sample, all significant effects disappear (the four P-values ranging from 0.23 to 0.39). However, in the lower part (hatching vs not hatching) the interaction between age at ringing and cause of remating remains significant at an even stronger level ($P = 0.012$). Data for these tests are given in Table 19.

Brood size and adoption

It is not very meaningful to discuss the relationship between final brood size and breeding success, because broods with a final size greater than zero are by definition successful. Furthermore, pairs losing their goslings are not necessarily unsuccessful, since many of the lost goslings apparently are not dead but adopted by other pairs. Similarly, adoption status of a brood tells little about breeding success for almost the same reasons. In addition,

Table 20. Returned goslings belonging to broods of different adoption status and final brood size. The return rate is a measure of survival during the first year. Utterslev Mose 1965-1993.
Antallet af gæslinger, der blev ringmærket 1965-1993, og antallet af dem der vides at have overlevet det første år ('returned'), grupperet efter hvorvidt de tilhørte kuld med adopterede gæslinger ('adoption'), og efter kuldstørrelsen ved sæsonens slutning ('brood size'). Ingen af disse forhold havde nogen signifikant effekt på andelen, der overlevede.

	Ringed	Returned	G_3	P
Adoption			3.25	0.35
none	941	431		
probable	334	171		
moderate	332	163		
extensive	597	285		
Total	2204	1050		
Brood size			1.64	0.65
1-4	520	250		
5-8	764	352		
9-15	629	311		
>15	314	148		
Total	2227	1061		



brood size and adoption status are closely interrelated (Fig. 23), so effects of brood size and adoption are essentially indistinguishable.

However, if large broods and adoption are mainly a privilege of the most dominant and competent pairs, it might well be that post-fledging goslings of large broods survive better than other goslings. They might for example have access to the best staging and feeding sites and so enjoy good feeding opportunities and protection against predators. If that is the case, subdominant pairs could in fact improve their own fitness by letting their offspring be taken over by dominant pairs.

In order to investigate this possibility, the return rate was determined for goslings belonging to broods of different final size and adoption status (Table 20). Most goslings (2227) ringed during 1965-1993 belonged to one of the broods (431 in total) for which the identity of one or both parents (or foster parents) was known, and for all but 7 of these broods the adoption status was known as well. However, not the slightest indication of a relationship between brood size (or adoption) and return rate was revealed by this procedure (Table 20), probably because no such relationship exists. The test was repeated for goslings sexed as females alone, but apart from the expectedly higher return rates overall, no other differences were apparent, and the conclusion remained the same.

However, since a large majority of the early broods were from the years 1989-1992 (see below), it was considered advisable to repeat the analysis for 1965-1988 alone. The sample was hereby reduced to 266 broods and 1360 ringed goslings, and the tests of Table 20 became, respectively, $G_3 = 5.12$, $P = 0.16$ (adoption), and $G_3 = 2.74$, $P = 0.43$ (brood size). The return rates behind the rather low significance level for an effect of adoption were 0.53, 0.48, and 0.50 for goslings having adoption scores 1, 2 and 3, respectively, or 0.50 overall, while for adoption score 0 it was 0.45. (In passing it may be noted again that broods assigned an adoption score of 1 seem to belong with

Table 21. Final size of broods in which the ringed goslings and the returned and recruited females grew up (recruited here means females that hatched at least one brood). Included are all goslings of known parents, Utterslev Mose 1965-1988, and returned (recruited) regular UM females. The G test compares the frequency distribution of brood size in the ringed sample and in the indicated sample (brood sizes grouped as 1-2, 3-4...17-18, and >18).
Gennemsnitlig slutstørrelse for kuldene i hvilke gæslinger voksede op. De tre betragtede grupper er alle de ringmærkede gæslinger ('ringed goslings'), de hunlige gæslinger der vides at have overlevet et år ('returned females'), og de hunlige gæslinger der vides senere at have ynglet ('recruited females').

Sample	Final size of brood where reared			G_9	P
	mean	SE	n		
Ringed goslings	8.20	0.13	1280	–	–
Returned females	8.42	0.30	279	6.27	0.71
Recruited females	8.22	0.43	129	4.45	0.88

Table 22. Adoption status of broods in which goslings grew up (same sample as in Table 21).
Adoptionsstatus for kuldene i hvilke gæslinger voksede op (samme grupper som i Tabel 21). Status: 0 ingen adoption, 1 formodentlig adoption af enkelte gæslinger, 2 sikker adoption af et moderat antal gæslinger, 3 adoption af et betydeligt antal gæslinger.

Sample	Adoption status of brood where reared				G_3	P
	0	1	2	3		
Ringed goslings	605	230	193	252	–	–
Returned females	135	47	43	51	0.45	0.93
Recruited females	67	20	19	21	1.66	0.65

scores 2 and 3 rather than with score 0.) A 2×2 test did in fact give a significant result ($G_1 = 4.08$, $P = 0.043$), even when applying the conservative Yates' correction ($G_1 = 3.86$, $P = 0.049$).

However, when considering females only – where survival and recruitment to the breeding population is more reliably estimated, since emigration is rare – and allowing enough time for the survivors to start breeding, a slightly different picture emerges. Table 21 shows that surviving and recruiting females came from broods the size of which did not differ from that of the average gosling. When adoption status is considered (Table 22), a similar result appears: any difference between the total sample of ringed geese and the returned/recruited females is small and statistically insignificant. If anything, there is a very slight over-representation of females from broods having adoption score 0, and an under-representation of those from broods with adoption score 3, especially in the sample of recruits.

Age of parents

The significance of age of female parent for brood size was discussed on p. 33-36, so the present section only explores the relationship between parent age and post-fledging survival of goslings.

As shown in the section on adoption of goslings (p. 37), relatively few broods with two known-age parents were available, so females and males were treated separately. The overall return rate of goslings of known-age female parents was 48.0%, and a relationship with female age was not immediately apparent (Fig. 24). Neither was a test with females grouped according to age significant (Fig. 25; $G_2 = 1.71$, $P = 0.43$). In goslings of known-age males, the overall return rate was 51.3%, and a higher return rate for goslings of middle-aged male parents was suggested (Fig. 24). This was confirmed when grouping the males: the test was almost significant

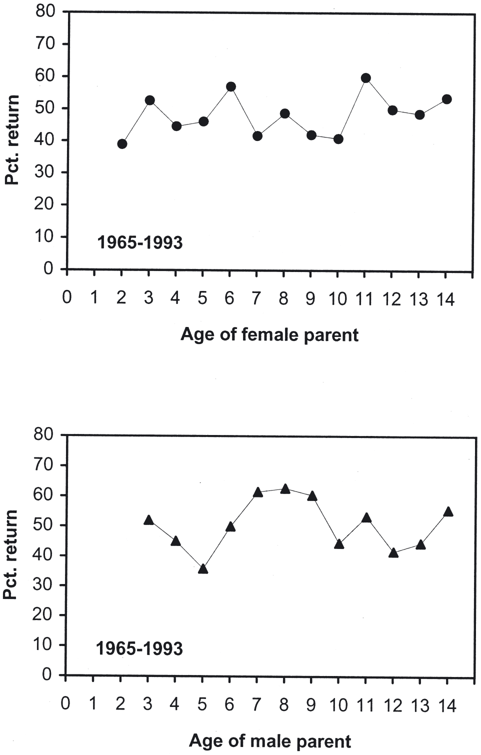


Fig. 24. Relationship between parent age and percent goslings that returned (i.e., were known to survive until the following spring). Female parents: r = 0.33, P = 0.27; 261 broods totalling 1245 ringed goslings, each return rate based on from 28-221 ringed goslings (4 broods and 11 goslings of females older than 14 years pooled with age 14). Male parents: r = 0.05, P = 0.87; 104 broods totalling 530 goslings, each return rate based on from 18-82 ringed goslings (3 broods and 8 goslings of 2-year old males pooled with age 3, 3 broods and 10 goslings of males older than 14 years pooled with age 14).
Gæslingernes tilsyneladende overlevelse fra ynglesæsonens afslutning til det følgende forår, plottet mod (øverst) moderens og (nederst) faderens alder. Der er ingen sammenhæng at spore (moderens alder: r = 0,33, P = 0,27; faderens alder: r = 0,05, P = 0,87).

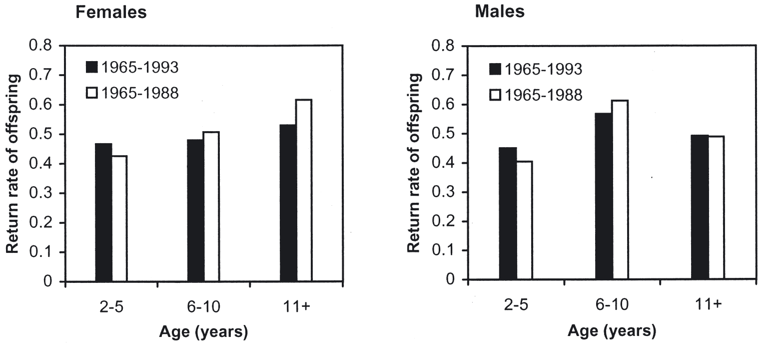


Fig. 25. Return rates of goslings of female and male parents belonging to different age classes. Because most of the years 1989-1993 were anomalous in some respects (see text), the results are shown both with and without the inclusion of these years. Females: n = 487, 624, 134 and 310, 339, 52; males: n = 171, 245, 114 and 89, 183, 88. *Retur-rater af gæslinger af hunner (females) og hanner (males) af forskellig alder (age) angivet i år. Vist både med og uden årene 1989-1993 (se teksten). Heterogenitet: 1965-1993 G_2 = 1,71, P = 0,43 (hunner) hhv. G_2 = 5,82, P = 0,055 (hanner); 1965-1988 G_2 = 8,52, P = 0,014 (hunner) hhv. G_2 = 11,23, P = 0,004 (hanner).*

(G_2 = 5.82, P = 0.055), primarily due to a high return rate (56.7%) of goslings of male parents aged 6-10 years (Fig. 25).

In the following section it is found that a large majority of the early broods are from the years 1989-1992. Since the goose population at Utterslev Mose was very large during these atypical years, and make up a considerable part of the dataset, a separate analysis for 1965-1988 appears warranted. In this case the overall return rate of goslings of ringed female parents was 47.9%, and a clear relationship with female age was indicated; with females grouped as before, the test result was G_2 = 8.52, P = 0.014 (Fig. 25). Young of ringed males had an overall return rate of 53.1%, and the difference between male age groups was significant (G_2 = 11.23, P = 0.004), primarily due to the high return rate (61.2%) of goslings of male parents aged 6-10 years.

It may be concluded that post-fledging survival and parent age are interrelated. Goslings of young parents have slightly poorer survival than goslings of middle-aged parents. For goslings of old parents (more than 10 years) the picture is more blurred: goslings of old mothers appear to survive better than those having middle-aged mothers, while goslings of old fathers seem to fare worse than goslings of middle-aged fathers. Chance may play a role here, since old parents are few. In the 1965-1988 sample, for example, there were 43 ringed goslings of fathers aged 12 years or more, but only six broods and three different fathers – one of them parented four of the broods. Corresponding numbers for female parents were 30 goslings, eight broods, and six different mothers (one parenting three of the broods).

Time of hatching

When mean initial brood size was regressed against 'hatching' date, a slope of -0.06 goslings per day resulted, corresponding to a decline in mean size from 6.71 on 17 April to 4.62 on 22 May (r = -0.567, P = 0.0004).

A relationship between hatching date and gosling survival to fledging cannot be established, however, owing to the widespread occurrence of adoption. There is a negative correlation between hatching date and apparent gosling survival, calculated as the total number of fledglings divided by the summed initial sizes of broods (17 April – 22 May, r = -0.505, P = 0.002). However, the apparent survival exceeds 100% on several days, especially in the early part of the period, indicating that the main reason is that adoption is more common in early broods. This interpretation is confirmed when mean adoption score is correlated with hatching date (r = -0.747, P = $3 \cdot 10^{-7}$).

There is a clear negative relationship between return rate and hatching date in the full sample (Fig. 26; r = -0.714, P = $9 \cdot 10^{-5}$, return rate decreasing by 1.2% per day). Contrary to expectation, the correlation is not improved by limiting the analysis to female goslings, where return rate is believed closely to approximate true survival (r = -0.540, P = 0.006, return rate decreasing by 1.0%

per day). Neither is the correlation improved in the sample of broods with no sign of adoption (not shown; $r = -0.612$, $P = 0.001$, return rate decreasing by 1.3% per day). A closer relationship might have been expected, because adopted goslings will not always be of the same age as their foster parents' own goslings (to which the 'hatching' date of the brood refers); but even though the ages differ, they are probably similar in a great majority of the broods, which has also been the general impression during the fieldwork. Also, the reduced sample is much smaller, 865 ringed goslings, against 2145 in the full sample.

Since post-fledging survival was found to be connected both with hatching date and parent age, it is not surprising that the two are interrelated. For female breeders there is a close correlation between age and mean hatching date up to an age of 7 years (1965-1993: $r = -0.993$, $P = 7 \cdot 10^{-5}$, slope -2.4 days per year; 1965-1988: $r = -0.985$, $P = 0.0003$, slope -2.6 days per year), after which the mean date varies without any trend. A similar pattern is seen in males (1965-1993: $r = -0.884$, $P = 0.019$, slope -2.0 days per year; 1965-1988: $r = -0.951$, $P = 0.003$, slope -2.2 days per year).

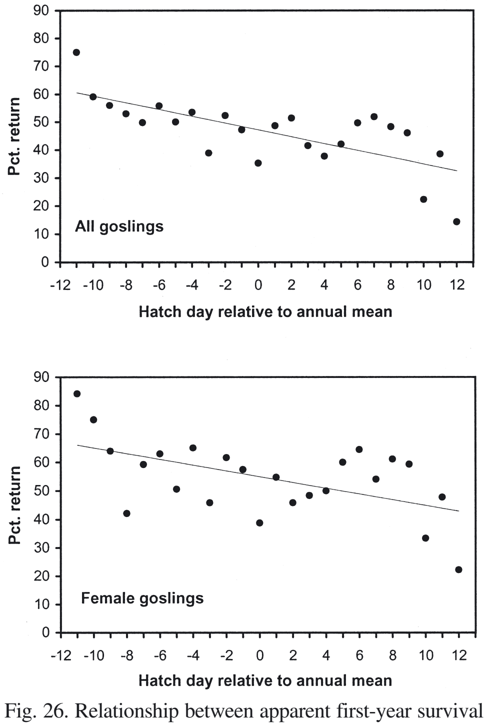


Fig. 26. Relationship between apparent first-year survival (return rate) and hatching day of goslings. Based on 2145 ringed goslings (1034 females) from 431 broods, 1965-1993.

Gæslingernes tilsyneladende overlevelse fra ynglesæsonens afslutning til det følgende forår, plottet mod klækningsdatoen (regnet relativt til årets gennemsnit). Øverst: alle ringmærkede gæslinger (r = -0,71, P = 0,0001); nederst: gæslinger, der blev bestemt til hunner (r = -0,54, P = 0,006).

Fledging weight

In the present study, 1803 sexed goslings (896 females, 907 males) were weighed at the ringing occasion during 1968-1993. The mean age was 43.4 ± 7.8 SD days (range 19-60 days) and almost equal for females (43.8 ± 7.7) and males (43.1 ± 8.0). Males are slightly heavier than females, so the two sexes were treated separately. To correct for age at weighing, weight was regressed against age and residuals calculated as the difference between actual weight and weight as predicted by the regression line. Inspection of the scatter around the regression line showed a symmetrical pattern for both sexes, except for the youngest goslings, 28 days or less. Since only 31 females and 49 males were that young, the linear approach was considered satisfactory. This regression line for females was $\text{weight} = 0.637 + 0.036 \cdot t$ kg, for males $\text{weight} = 0.476 + 0.045 \cdot t$, predicting a mean weight on day 40 of 2.078 ± 0.304 kg for females, 2.270 ± 0.341 kg for males (the standard deviation being that of residuals for all ages). It appears that although males are heavier, there is a considerable overlap between the two sexes.

For similar reasons as in the previous section, adoption is a nuisance factor, and the relationship between gosling weight and survival is explored using both the full available sample and the reduced sample obtained by disregarding all broods in which adoption occurred. The reduced sample contained 360 females and 384 males with a mean age at ringing of 41.4 ± 8.1 and 40.6 ± 8.8 days, respectively. The regression lines were $\text{weight} = 0.479 + 0.041 \cdot t$ kg (females) and $\text{weight} = 0.262 + 0.050 \cdot t$ (males), predicting a mean weight on day 40 of 2.124 ± 0.313 kg for females, 2.275 ± 0.328 kg for males.

The goslings were pooled in weight-classes each spanning 200 g in weight residual, and apparent survival (number known to have survived one year divided by number ringed) calculated for each class (Fig. 27). As expected, the lightest goslings had poorer survival than others, although the few birds in the -0.8 kg weight class and below weaken the conclusion (14 females, 21 males in total; 11 females, 5 males without adoption). In the total sample, females having residuals between

-0.6 and +0.4 kg, and males between -0.6 and +0.2 kg, show a linear growth in survival with weight, albeit not quite statistically significant (females: r = 0.794, P = 0.059, slope = 12% per kg; males: r = 0.740, P = 0.152, slope = 16% per kg). When disregarding broods where adoption occurred (bottom graph of Fig. 27), the pattern is similar – and significant –in females (r = 0.838, P = 0.037, slope = 11% per kg), whereas in males a *negative* relationship becomes apparent throughout the range of residuals (r = -0.736, P = 0.037, slope = -12% per kg).

For heavier goslings in the total sample, the pattern is puzzling. If the low survival of females having weight residuals around +0.6 kg is spurious, the increasing tendency may seem to continue, even though only 11 ringed females belonged to the heaviest class (+0.8 kg). There were 30 females in the apparently abnormal +0.6 kg class, and curiously, 14 were ringed in three years only (1977, 1980, 1982), with only two of these (from 1982) known to have survived. All three 1977-females were brood-mates, and 6 of the brood's 10 goslings survived, while three 1980-goslings were from a large brood of 17, of which only 3 are known to have survived. Whatever this may mean, such a concentration to certain years could impair the independence of observations, so it may tentatively be concluded that the heaviest females survive as well as slightly lighter females. In the total sample of males, however, there is no obvious way of explaining away the dip in the curve after the +0.2 kg class – the heaviest class comprised two ringed males only and tells us nothing, but the three other points are based on 100, 46, and 18 ringed males, respectively, without any apparent anomaly in distribution over years. And in the reduced sample, a negative relationship between fledging weight and apparent survival was fairly distinct and even statistically significant. However, that heavy male goslings should actually survive poorly must be considered highly unlikely; but they could be more prone to emigrate and settle somewhere else than at Utterslev Mose, although the reason for such a tendency is not obvious.

Body mass and time of hatching appears to be weakly interrelated so that earlier hatched goslings on average are heavier than late goslings, as shown in Fig. 28 for female goslings from broods with no adoption. However, although the correlation between individual (relative) hatch day and weight residual is significant (Fig. 28, top; r = -0.199, n = 359, P = 0.0001), the correlation between mean weight residual and hatch day is not (Fig. 28, bottom; r = -0.314, n = 21, P = 0.17). Similar results are obtained with other subsamples (males, either sex with inclusion of adopted goslings).

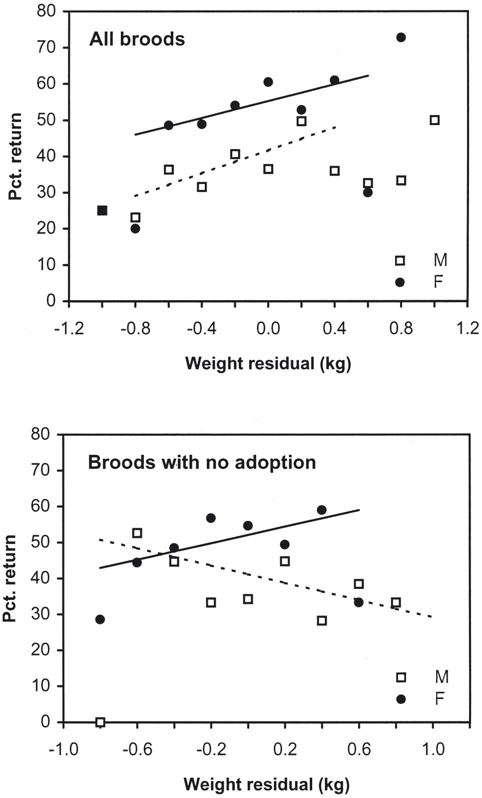


Fig. 27. Relationship between residual fledging weight and apparent survival in female (F) and male (M) Greylag Geese ringed as goslings, 1968-1993. Top: full sample of weighed goslings (895 female and 907 male goslings). Bottom: sample limited to goslings from broods where adoption did not occur (359 female and 384 male goslings). Regression lines for females (full-drawn) are based on the range -0.6 – +0.4 kg, for males (broken) on -0.6 – +0.2 (top) or -0.6 – +0.8 (bottom).
Gæslingernes tilsyneladende overlevelse fra ynglesæsonens afslutning til det følgende forår, plottet mod vægten ved ringmærkningen (angivet som afvigelsen fra den normale vægt for den alder de havde på mærkningstidspunktet). Hunner er markeret med fyldte cirkler, hanner med firkanter. Øverst: hele materialet. Nederst: kun gæslinger fra kuld ikke berørt af adoption. For dele af vægtområdet i øverste delfigur er der tilsyneladende en positiv sammenhæng mellem vægt og overlevelse for begge køn, men den er ikke signifikant (hunner: r = 0,79, P = 0,06; hanner: r = 0,74, P = 0,15). I nederste delfigur er der en tilsvarende og signifikant tendens for hunner (r = 0,84, P = 0,04), og samtidig en negativ tendens for hanner over hele vægtområdet (r = -0,74, P = 0,04).

Weight residual was also related to the age of the mother, but in a limited way only: 2-3 year old females had lighter goslings than other females (grouped as 4 years old, five years or older, and ringed as adults), both in the full 1968-1988 sample and in the subsample with no adoption (only goslings sexed as females considered; P < 0.05 in all cases). Differences between the other groups were not significant. In the much smaller sample of goslings with known-age fathers, a similar result was obtained, except that the difference between goslings of 2-3 year old fathers and other goslings in broods with no adoption was statistically significant only in the comparison with goslings of adult-ringed fathers. In this light it is not surprising that correlation coefficients between female or male parent age and weight residual were very small and far from significance.

The correlation between annual mean weight residual and mean brood size was not significant, but if only early broods were considered (hatched before the mean date of the year), the significance level was rather low, and the relationship was negative (lighter goslings in large broods; females 1965-1988: r = -0.37, P = 0.18).

Finally, when looking at the relationship between weight residual and adoption score of the brood, it appeared that the heaviest goslings were those from broods having an adoption score of 1, followed by scores 0, 2 and 3, in that order. Goslings with scores 0 and 1 were significantly heavier than those having scores 2 (P < 0.05) and 3 (P < 0.001), whereas the difference between 0 and 1, and between 2 and 3, was not significant. Gosling weight was actually the only characteristic that united broods of score 1 with those of score 0 instead of those of scores 2 and 3. One possible explanation could be that adopted goslings, on average, were slightly younger than the foster parents' own offspring.

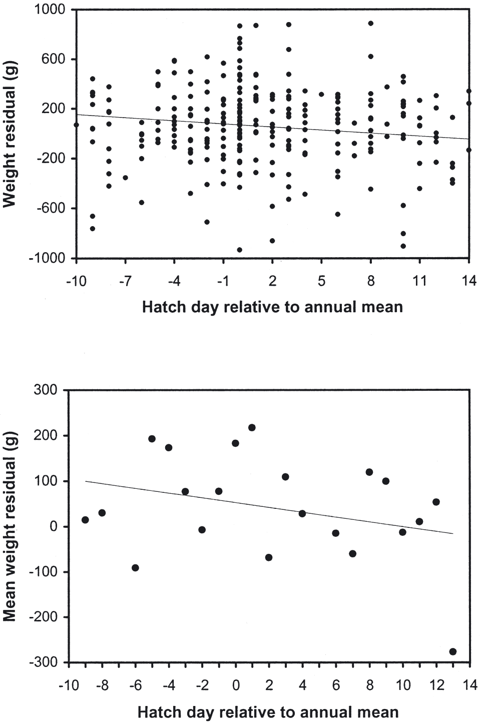


Fig. 28. Relationship between hatching day and weight residual. Female goslings from broods with no sign of adoption, 1968-1993. Top: individual gosling weights (n = 359). Bottom: annual mean weights.
Sammenhæng mellem klækningsdato og vægtafvigelse i forhold til normen for gæslingerne (kuld uden tegn på adoption, 1968-1993). Datoerne er angivet som antallet af dage mellem ungens klækning og årets gennemsnitsdato. Øverst: individuelle vægte (n=359). Nederst: gennemsnitsvægte for hver af de betragtede datoer. Tendensen mod lavere vægt for sene kuld er signifikant for de individuelle vægte (r = -0,20, P = 0,0001), men ikke for gennemsnitsvægtene (r = -0,31, P = 0,17).

An alternative way of viewing fledging weights

It is possible to approach the question of gosling weight and its implications in another way. The sample can be subdivided into four natural groups: 1) UM, the goslings that survived and settled at Utterslev Mose. 2) Emigr., the goslings that survived but settled somewhere else. 3) Rec1, the goslings that were recovered (mostly as shot) during their first year of life. And 4) Rest, all other goslings, either dead but not recovered, or emigrated and never heard of since. The UM group is biased towards females, while Emigr. and, to a lesser extent, Rest are biased towards males. The female and male subsamples are defined by the sex as scored at ringing, and the UM 'males' contain many mis-sexed females (and the UM 'females' few mis-sexed males). If mis-sexed birds are representative of their true sex as regards weight (which may not be true), the UM 'males' ought to be rather light, and the UM 'females' normal or perhaps slightly light, compared to the total sample. In the Emigr. and Rest samples the roles of the sexes are reversed, while no sex bias, hence no weight deviation from the total sample, is expected for the Rec1 sample. A deviation from this predicted pattern might tell something about the relative survival of different weight-classes.

It appears from Table 23 that, contrary to the above predictions, females in the Rest group are

Table 23. Mean and standard deviation of weight residuals (grams) of Greylag Geese belonging to different groups. All were ringed as goslings and weighed at ringing. UM: geese that returned to Utterslev Mose after one or more years, i.e., survived their first year. Emigr.: emigrants, geese that survived the first year but did not settle in Utterslev Mose. Rec1: geese recovered dead during their first year of life. Rest: all birds not included in any other group, a mixture of birds that died without being recovered, and survivors not recovered or recorded as visitors in Utterslev Mose. Three of the samples have a biased sex distribution. See Table 24 for statistical tests.
De unge-mærkede Grågæs opdelt i fire grupper: UM, dem der slog sig ned i Utterslev Mose; Emigr., de øvrige fugle der vides at have overlevet det første år; Rec1, de fugle, der er genmeldt i deres første år; og Rest, alle andre, dels døde men ikke genmeldte, dels overlevende som hverken er set eller genmeldt siden. 'Bias' angiver det køn, der i pågældende gruppe er overrepræsenteret i forhold til den samlede gruppe af mærkede fugle (Total): hunner (female), hanner (male), eller ingen af dem (none). Da hanlige gæslinger i gennemsnit er tungere end jævnaldrende hunlige gæslinger, og da ca 10% af gæslingerne bestemmes til galt køn, vil UM gruppen fx rumme relativt færre fejlbestemte 'hunner' (dvs. hanner) og flere fejlbestemte 'hanner' (dvs. hunner) end den totale gruppe; ungevægten bør derfor også være relativt lav. Noget tilsvarende, med modsat fortegn, gælder grupperne Emigr. og Rest. Disse forventninger til gennemsnitsvægten (exp. deviation) er gjort under den forudsætning, at vægten ingen indflydelse har på overlevelsen. De observerede afvigelser er små, men i en retning der tyder på dårligere overlevelse for lette end for tunge gæslinger. De påfaldende tunge gæslinger i Emigr. gruppen tyder desuden på, at de tungeste hanner er mest tilbøjelige til at slå sig ned andre steder end deres fødested, Utterslev Mose. Se Tabel 24 for statistiske tests.

	UM	Emigr.	Rec1	Rest	Total
Bias	female	male	none	male	none
Ringed as females					
Exp. deviation[1]	(–)	+	0	+	0
All					
Mean	10.76	15.84	25.77	-19.20	0.00
StDev	284.59	337.54	295.68	328.31	304.42
N	466	22	55	353	896
No adoption					
Mean	16.58	167.42	3.48	-29.15	0.00
StDev	289.21	429.14	287.81	339.83	312.62
N	183	6	29	142	360
Ringed as males					
Exp. deviation[1]	–	(+)	0	(+)	0
All					
Mean	-5.34	86.12	13.77	-11.16	0.00
StDev	329.06	294.57	345.09	351.91	340.73
N	282	70	67	488	907
No adoption					
Mean	-58.95	128.63	117.35	-2.46	0.00
StDev	323.20	305.35	339.78	325.32	328.37
N	114	28	31	211	384

[1] Expected weight (residual) deviation relative to the total sample under the assumption that survival is independent of weight

lighter than in the total sample, while females in all the other groups are heavier. This pattern seems to indicate that light females survive poorly. The differences between groups are small, however, and none is statistically significant (Table 24). Males belonging to the Rest group are also light, again apparently indicating a poor survival of light goslings. UM males are light, as predicted, but the difference from the total sample is small, again suggesting that many of the lightest males died. However, the males in the Emigr. group are markedly heavier than other males, a further indi-

Table 24. Tests of differences between the weight residuals shown in Table 23. Above diagonals: t-values. Below diagonals: P-values. In three cases where the compared samples had unequal variances, the P' is shown as well.
Test af vægtforskellene mellem grupperne vist i Tabel 23. Over diagonalerne står t-værdier, under står signifikansniveauer. De eneste forskelle, der er signifikante på 5%-niveauet, er at for gæslinger bestemt til hanner er Emigr.-gruppen tungere end UM og Rest grupperne, og med gæslinger fra kuld berørt af adoption udeladt er desuden Rec1 gruppen tungere end UM gruppen (mens sammenligningen med Rest næsten er signifikant).

	All				*No adoption*			
	UM	Emigr.	Rec1	Rest	UM	Emigr.	Rec1	Rest
Ringed as females								
UM		0.081	-0.368	1.396		1.237	0.227	1.309
Emigr.	0.935		-0.128	0.485	0.217		1.167	1.374
Rec1	0.713	0.899		0.957	0.821	0.252		0.483
Rest	0.163[1]	0.628	0.339		0.191[3]	0.172	0.630	
Ringed as males								
UM		2.123	-0.423	0.227		2.781	-2.664	-1.497
Emigr.	0.034		1.322	2.204	0.006		0.134	2.017
Rec1	0.672	0.189		0.545	0.009	0.894		1.904
Rest	0.821	0.028[2]	0.586		0.135	0.045	0.058	

[1] P' = 0.172
[2] P' = 0.013
[3] P' = 0.201

cation that heavy males may tend to emigrate rather than settle in their natal Utterslev Mose. In fact, the only differences between the male groups in the full sample that are statistically significant are those between the heavy Emigr. group and, respectively, the Rest and the UM group (Table 24). The male Emigr. group is also heavier than the total sample ($t_{975} = 2.056$, $P = 0.04$), whereas all other comparisons between any group and the total in both sexes are non-significant (P between 0.33 and 0.82). In the reduced sample the same tendencies are apparent and even amplified, and for some reason also the recovered males appears to be heavy. The deviation from the total sample of ringed males is significant or nearly significant in all groups but Rest (UM: $t_{496} = -1.689$, $P = 0.09$; Emigr.: $t_{410} = 2.010$, $P = 0.05$; Rec1: $t_{413} = 1.909$, $P = 0.06$; Rest: $t_{593} = -0.080$, $P = 0.93$).

It may finally be noted that the annual mean weights of goslings vary, for a large part because mean age at ringing varies with year (from 35 days in 1980 to 51 days in 1991, although most years are much closer to the overall mean of about 43 days). This makes direct comparisons of weight (instead of weight residual) unreliable, because the four groups do not contribute in the same proportions throughout the study period ($G_{51} = 135.93$, $P = 10^{-9}$). The Rec1 group is the earliest (mean year 1978.4), followed by Emigr. (1979.9), UM (1982.6), and Rest (1982.8). The annual mean residual weights and mean ages at ringing, as would be expected, are not correlated (females $r = -0.155$, $P = 0.51$; males $r = -0.236$, $P = 0.32$, with similar results in the reduced sample).

Recruitment

Since the conditions experienced by goslings may mark them for life, the factors that could be supposed to affect survival may also influence success in obtaining breeding status. This possibility is explored for females in Table 25 (cf. also Table 21-22), considering various characteristics of the parents and the brood in which the female grew up, while the possible effect of gosling body mass is addressed for both sexes in Table 26. None of the factors considered in Table 25 had any clear effect, except for an apparent – and unexpected – advantage of being hatched near the mean date. A few other, minor effects are suggested as well, but could not be demonstrated in the present sample, and my not exist at all. In the "cleaner" sample of broods apparently not containing adopted goslings, it looks as if late-hatched females and fe-

Table 25. Relationship between recruitment and characteristics of broods in which female Greylag Geese grew up. Included are regular Utterslev Mose geese ringed 1965-1988 and attaining an age of at least 2 years (all definitively sexed as females). Recruited females in this context are those that hatched at least one brood. All tests are G-tests of contingency tables.

Rekruttering (%) til ynglefuglenes rækker blandt overlevende, unge-mærkede hunner fra kuld grupperet efter forskellige kriterier: klækningsdato relativt til årets gennemsnit ('hatch date'), alderen af moderen ('age of mother') og faderen ('age of father'), størrelsen af kuldet de voksede op i, i starten og ved slutningen af ungeføringsperioden ('initial' hhv. 'final size of brood'), samt hvorvidt kuldet var involveret i adoption eller ej ('adoption').

	All females			Females from broods with no adoption			Test, comments
	n	Pct. recruited	P	n	Pct. recruited	P	
Hatch date[1]							
-5 or before	48	41.7		19	63.2		df = 4
-4 to -2	76	51.3		28	50.0		but mid-group vs
-1 to +1	57	61.4		30	70.0		others (df=1):
+2 to 8	60	45.0		29	48.3		G=4.18, P=0.041 all
9 or more	26	42.3		18	33.3		G=4.17, P=0.041 n.adp.
Total	267	49.4	0.23	124	54.0	0.11	
Age of mother (years)							
2-4	27	51.9		15	40.0		df = 2 (test excludes
5-7	60	55.0		38	60.5		ad.-ringed)
8+	46	47.8		25	52.0		
Ad.[2]	123	46.3		40	55.0		
Total	256	49.2	0.76	118	54.2	0.39	
Age of father (years)							
2-4	13	53.8		6	50.0		df = 2 (test excludes
5-7	17	41.2		7	28.6		ad.-ringed)
8+	53	37.7		15	46.7		
Ad.[2]	162	53.1		85	57.6		
Total	245	49.0	0.58	113	54.0	0.66	
Initial size of brood							
1-3	19	52.6		15	53.3		df = 3
4-6	115	51.3		72	52.8		
7-9	65	52.3		35	57.1		
10-12	36	36.1		2	50.0		
Total	235	49.4	0.38	124	54.0	0.98	
Final size of brood							
1-3	29	44.8		27	44.4		df = 4 and 2
4-6	85	58.8		70	58.6		
7-9	50	50.0		27[3]	51.9		
10-12	40	45.0					
13+	61	41.0					
Total	265	49.4	0.25	124	54.0	0.44	
Adoption							
Yes	139	44.6					df = 1
No	124	54.0					
Total	263	49.0	0.13				

[1] Relative to annual median day

[2] Ringed as adult

[3] One female from a brood of 10 included

Table 26. Relationship between recruitment and body mass at ringing for regular Utterslev Mose geese ringed 1965-1988 (definitely sexed birds attaining an age of at least two years). Recruited birds in this context are those that hatched at least one brood.
Sammenhæng mellem vægt ved ringmærkningen og senere rekruttering (%) af overlevende, unge-mærkede gæs (jf. Tabel 25). Kun fugle mindst to år gamle og sikkert kønsbestemt som voksne er betragtet.

Weight residual (grams)	All birds			Birds from broods with no adoption		
	n	Pct. recruited	P[1]	n	Pct. recruited	P[1]
Females						
< -100	64	50.0		28	50.0	
-100 – 100	62	40.3		30	53.3	
> 100	65	63.1		35	62.9	
Total	191	51.3	0.035	93	55.9	0.557
Males						
< -100	23	34.8		8	25.0	
-100 – 100	18	22.2		7	14.3	
> 100	23	30.4		9	22.2	
Total	64	29.7	0.673	24	20.8	0.865

[1] G-tests

males of young mothers are at a disadvantage even when they have survived for a few years. In the full sample a disadvantage is suggested of belonging to a brood that was enlarged by adopted young. If this really is the case, it would be interesting to know if this disadvantage is shared by all brood members, or if the adopted young alone bear the burden. Unfortunately, however, in the present data it is not possible to distinguish between the parents' own goslings and those that were subsequently adopted.

In Table 26 the heavy females appear to be more successful in entering the ranks of the breeders than light and average females. Curiously, however, mid-weight females (full sample) have the poorest recruitment, but the difference between the two lightest groups is not significant ($G_1 = 1.19$, $P = 0.27$), whereas these two groups combined have lower recruitment than the heavy group ($G_1 = 5.51$, $P = 0.02$). No such effect is suggested for males, possibly because of the small samples. However, in the previous section the possibility was raised that heavy males were more prone to emigrate than lighter males. It is therefore possible that many heavy males settled elsewhere after having spent one or a few seasons as youngsters at Utterslev Mose; in the applied classification, they would have been regarded as regular males dying early rather than emigrants unless they showed up occasionally in later years. Emigration and failed recruitment may thus to some extent be confounded in the same way as emigration and survival.

Lifetime reproductive success of females

In order to determine the lifetime reproductive success (LRS) of birds, and especially the variation between individuals, it is necessary to limit the sample to cohorts from which no birds are still alive by the end of the study. If not, the proportion of younger birds, producing no or few young, will be inflated. In the Utterslev Mose goose study this means that only the subsample of birds ringed as goslings till and including 1981 is available. The sample size is hereby limited to less than half of the full sample, which is one reason that only females are considered in the following. However, the main reason for not attempting to estimate the LRS for males is that the record for males is very incomplete, since a significant proportion of the males emigrated. In females, a large majority have been followed throughout their adult life.

Ideally, all female fledglings should be followed until their death, and their production of fledged offspring recorded. However, the dataset does not permit this to be done directly. First, the goslings were not sexed with certainty, so we do not know the exact number of females. Furthermore, for a considerable number of goslings during the early years sexing was not even attempted, and omitting unsexed goslings would further limit the sample size by a fourth. Instead, gosling numbers were corrected using probabilities as described in Appendix 1, and unsexed goslings were assumed to have the same sex distribution as the sexed goslings. Neither in the full sample nor in any subsample did the sex distribution of goslings deviate significantly from parity, but the consistency of a small male bias made the procedure preferable to simply assuming that half of the goslings were female.

The second difficulty is that many goslings were adopted by other pairs before fledging, rendering number of fledged goslings an unreliable measure of breeding success. The LRS in the following is therefore based on number of hatched goslings (brood size when first seen). The overall survival from hatching to fledging was previously given as roughly 90%, which value could be applied if wishing to express LRS in terms of number of fledglings produced.

The estimated number of female goslings leaving Utterslev Mose during the years 1959-1981 is given in Table 27, together with the number known to have survived the first year, broken down according to the sex score given at ringing. From

Table 27. Number of goslings ringed in Utterslev Mose (UM) 1959-1981, and number known to have survived the first year of life. Total numbers are subdivided according to sex as determined at the ringing occasion, and to true sex. Proportion mis-sexed goslings is estimated as described in Appendix 1.
Gæslinger fra årene 1959-1981, som alle havde en afsluttet historie, da undersøgelsen sluttede i 1994. Antal ringmærket, estimeret andel der blev fejlagtigt kønsbestemt, og de heraf følgende 'sande' mærkningstal af de to køn, samt antallet der overlevede det første år og slog sig ned i Utterslev Mose eller som emigrerede, inddelt efter køn som bestemt ved mærkningen og sandt køn ('true sex').

	Sex as determined at ringing[1]			Total
	Female	Male	unknown	
Number ringed	591	612	409	1612
Proportion mis-sexed	0.116	0.110		
Estimated number	794	818		1612
Returned to UM				
True females	190	25	64	279
True males	12	97	42	151
Unknown sex	62	65	30	157
Emigrants				
True females			2	2
True males		7	5	12
Unknown sex	20	62	39	121

[1] Except for the third row, where distribution according to true sex is estimated

Table 28. Estimated sex distribution of the 587 yearlings returned to Utterslev Mose (UM) and the 135 emigrants (cf. Table 27). The female bias of the UM sample means that the proportion mis-sexed 'females' is much smaller than in the entire sample of sexed goslings, whereas the proportion mis-sexed 'males' is much greater (see Appendix 1).
Estimeret kønsfordeling blandt de 587 UM-gæs og de 135 emigranter i Tabel 27. Øverste række er den estimerede andel af oprindeligt fejlbestemte hunner og hanner blandt de fugle, der slog sig ned i Utterslev Mose.

	True sex[1]		Total
	Female	Male	
Proportion mis-sexed (UM)	0.059	0.205	
Estimated numbers			
UM	369	218	587
Emigrants	33	102	135
Total	402	320	722

[1] Except in the first row, showing estimated proportion of 'female' ('male') goslings that actually were males (females)

Table 29. Number and production of goslings of females ringed as goslings 1959-1981 and settling in Utterslev Mose (of the 369 in Table 28, the rest disappearing before becoming properly established).
Antal og ungeproduktion hos gruppen af unge-mærkede hunner (1959-1981), der slog sig ned i Utterslev Mose (UM gruppen i Tabel 28). Resten af de skønnede 369 fugle forsvandt inden de blev rigtig etablerede i mosen, formentlig i næsten alle tilfælde fordi de døde. De fleste etablerede forblev i mosen, men en mindre del('irregular') ynglede åbenbart i nogle år andre steder, hvorfor kendskabet til deres reproduktion (klækkede 'hatched' og flyvefærdige 'fledged' gæslinger) er ufuldstændigt.

	Regular	Irregular	Total
UM females	262	17	279
Hatched goslings	1570	≥82	≥1652
Fledged goslings	1380	≥64	≥1444

these numbers, the actual numbers can be estimated by assessing the number of females and males among the unknowns (Table 28). In so doing, the probabilities in Table 28 were used for unknowns having been sexed as goslings, while unknowns not having a sex score were assumed to have the same sex distribution as the other returned birds. For the emigrant group we do not have similar probabilities of being mis-sexed on which to base a correction, and furthermore, in this sample the number of sexed birds was very low. The emigrant group is certainly male biased, so in the absence of any better option, the procedure from the UM group was repeated, but with the probabilities of Table 28 reversed. To check this slightly roundabout way of arriving at the number of females surviving their first year, we may note that the 402 returned females make out 51% of the 794 ringed. Compared with previously given estimates for the first-year survival of female-ringed goslings (Fig. 10; see also Appendix 2) this figure appears to be a little low, but well within reasonable limits. The rather uncertain estimate of the number of emigrants correspond to 4%, which also looks reasonable. The implication of course is that practically all surviving females were recorded at some time, which at a first glance may seem improbable. However, Nilsson & Persson (2001a) found that none of the neck-collared females in a population of Greylag Geese in southern Sweden settled outside a radius of 7 km from their natal site. If the same is true for UM females, it would not be unreasonable if most of the emigrants would occasionally be seen at UM.

Of the about 369 non-emigrant surviving females, 279 settled at UM long enough and under circumstances where they could be reliably sexed (Table 29). The remaining c. 90 females disappeared, almost all probably because they died. They make up 24% of the total, largely corresponding to the expected second-year mortality of these geese (cf. also Appendix 2). A few could of course have emigrated, and the distinction between such birds and 'emigrants' is rather artificial. But as suggested above, emigrant females are likely to turn up at UM from time to time, and at any rate, the emigrant group already appears to be about as large as it could reasonably be.

Table 29 also gives the number of goslings hatched and fledged by the UM females. The irregular UM females spent part of their adult life at Utterslev Mose and part at some other locality, and the record of their breeding output hence is almost certainly incomplete. The total number of hatchlings thus was at least 1652, and probably somewhat higher. If the irregular UM females and the emigrants produced as well as the regular UM females, the total number of hatchlings would be 1811, corresponding to about 1620 fledglings if 90% of the goslings survived. This almost exactly equals the 1612 fledglings from which these females derive. Since the net growth in the population during these years was almost nil (Fig. 3), this would seem to be as it should be. However, some of the fledglings were produced after 1981, so the

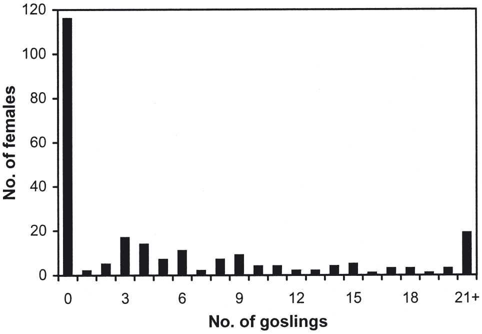


Fig. 29. Reproductive success (goslings hatched) of 241 females ringed as goslings during 1959-1981 and surviving to at least the age of two years.
Antal gæslinger ('No. of goslings') klækket af 241 hunner, der blev ringmærket som gæslinger i årene 1959-1981 og overlevede frem en alder af mindst to år. Næsten halvdelen, 116 hunner, producerede ikke en eneste gæsling.

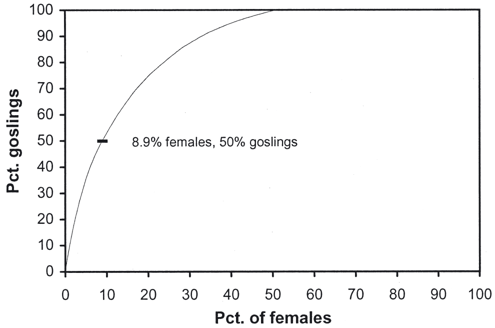


Fig. 30. Cumulative proportion of goslings hatched by the females in Fig. 29, with females ordered from the most productive downwards. 51.9% of the females succeeded in producing at least one gosling; of these, 17.2% produced 50% of the goslings.
Procentdelen af gæslinger produceret af hunnerne i Fig. 29, når disse medtages i rækkefølge fra de mest til de mindst produktive. 50% af gæslingerne blev produceret af 8,9% af hunnerne (17,2% af de hunner, der fik mindst én unge).

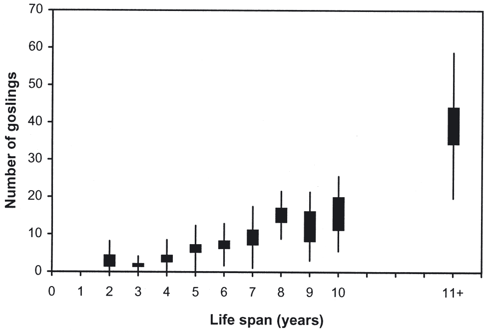


Fig. 31. Goslings hatched by female geese enjoying different life spans (same sample as in Figs 29-30). Mean number of goslings per female is shown plus/minus one standard error and one standard deviation. Mean life span of the 11+ group was 13.9 years.
Gæslinger produceret gennem livet af hunner, afsat mod hunnernes levetid: gennemsnit ± standardfejl og standardafvigelse (samme hunner som i Fig. 29-30). Den gennemsnitlige levetid for 11+ gruppen var 13,9 år.

accordance between fledgling numbers in the two generations cannot in itself be taken as an indicator of the quality of the data, or of the validity of the underlying assumptions.

Of the 262 regular UM females in Table 29, 21 disappeared after one year, while the remaining 241 survived long enough to have the chance to breed. In addition, a few of the geese never sexed after returning also survived to the age of two years, and 15-20 of them may have been females; since the exact number is unknown, and none of these birds bred, they are ignored, i.e., treated as having died before their second spring. The performance of the 241 surviving females is summarised in Table 30, with that of adult-ringed females shown for comparison. It appears that the main difference between females ringed as goslings and those ringed as adults is that the former on average hatched goslings in only half as many seasons as the latter, and got half as many hatchlings during their lifetime. The difference must actually be greater than it appears, because

Table 30. Breeding performance of female Greylag Geese in Utterslev Mose: number of years from the age of 2 years to death (for adults from ringing to death), number of years breeding, number of years hatching goslings, and total number of goslings hatched. Total years as defined is equivalent to potential number of breeding years.
Levetid og ynglesucces hos regelmæssige UM hunner mærket som unger 1959-1981, og hunner mærket som adulte 1959-1993 (separat er desuden vist de adult-mærkede, der var døde ved undersøgelsens afslutning). Vist er levetiden efter det andet år ('total years'), hvilket er det potentielle antal ynglesæsoner, fuglene kan have haft; antal sæsoner hvor de ynglede ('breeding years'); antal sæsoner hvor de fik unger ('hatching years'); og det samlede antal gæslinger de klækkede ('No. goslings'). Kun hunner, der blev mindst to år gamle, er medtaget.

Regular UM females ringed as	Total females	Total years			Breeding years			Hatching years			No. goslings		
		mean	SD	range	mean	SD	range	mean	SD	range	mean	SD	range
Goslings 1959-81	241	4.01	3.09	1-17	2.20	2.70	0-14	1.31	1.93	0-11	6.51	11.30	0-71
Adults 1959-93	130[1]	3.99	2.95	1-16	2.82	2.32	0-9	2.19	1.87	0-8	12.31	11.78	0-61
- dead by 1994	111[2]	3.80	2.99	1-16	2.69	2.20	0-9	2.13	1.83	0-8	12.10	11.71	0-61

[1] number of goslings based on 127 females with complete records
[2] number of goslings based on 108 females with complete records

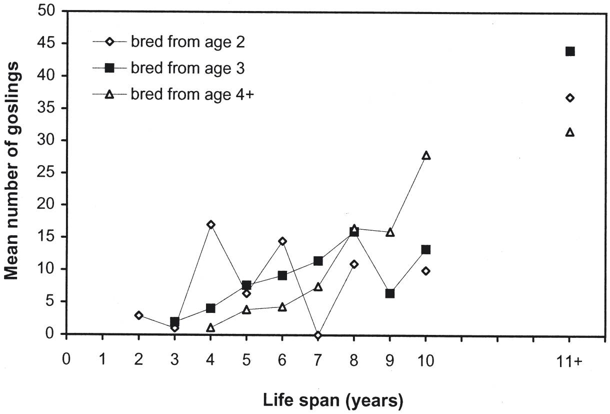


Fig. 32. Mean number of goslings hatched per female vs life span and breeding start of female. Same sample as in Figs 29-31. *Gæslinger produceret gennem livet af hunner, afsat mod hunnernes levetid for hunner, der først ynglede som 2-årige (romber), som 3-årige (fyldte firkanter), og som 4-årige eller senere (trekanter). Samme hunner som i Fig. 29-31.*

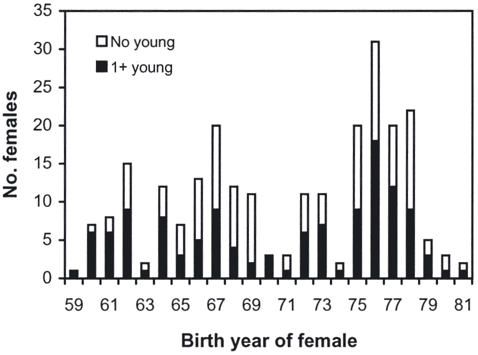
some of the adult-ringed females had almost certainly bred before they were ringed. The main reason for the poor performance of those ringed as goslings is that it takes several years for a goose to become a fully competent breeder – based on various parameters presented in previous sections this does not happen until the age of about six years. This is a respectable age for a goose, and many will have died before becoming that old.

Against this background it is not surprising that there is a tremendous variation in the number of young produced by the geese (Fig. 29; cf. also the large standard deviations and ranges in Table 30). An alternative way of visualising the skewness is shown in Fig. 30. Almost half (116) of the 241 females that survived to the age of two years never succeeded in hatching a brood, while at the other extreme one female (# 2473, from 1972) hatched 71 goslings in 10 seasons during her lifetime of 13 years. Furthermore, the 241 females comprise only about 65% of those surviving the first year (cf. Table 28). They also comprise only 30% of the 794 that fledged, but some of these survived and settled to breed at sites other than Utterslev Mose.

When looking for determinants of young production – factors making females successful – life span is an obvious candidate; a long life must be at least a necessary condition for a high reproductive output, if not a sufficient one, since the number of goslings per season is limited to about 10. This is borne out by Fig. 31, and although the variation between females having similar life spans is large, the correlation between LRS (goslings produced) and life span is fairly strong ($r = 0.77$ for the 241 females surviving to at least two years; $r = 0.71$ for the 125 of them that produced at least one gosling). In other words, life span explained 60% (r^2) of the variation in LRS.

Breeding start could be another factor, an early start at least, if successful, guaranteeing some offspring in case of a short life span. However, any advantage of an early start appears to disappear after the sixth or seventh year of life (Fig. 32). The birth year of a female might also influence her future reproductive success, because post-fledging survival varies between years to some extent, and because the survivors may be in better health and general body condition in some years than in others, a condition that conceivably could mark a female for the rest of her life. However, at least in terms of producing or not producing young, no marked difference between females born in different years is apparent (Fig. 33), except that females born during the late sixties performed poorly (all years with more than three females: $G_{15} = 40.75$, $P = 0.0003$; disregarding 1965-1969: $G_{10} = 8.12$, $P = 0.62$; 1965-1969 alone: $G_4 = 2.57$, $P = 0.63$; 1965-1969 combined vs other years combined: $G_1 = 8.00$, $P = 0.0047$). The apparently very high proportion of surviving females that bred successfully during the first years of the study might be real, although the possibility that some failed breeders and non-breeders were overlooked cannot be excluded; survey routines were not as firmly established then as they became later, and the geese were much more shy in the sixties than in later years.

Fig. 33. Proportion of females hatching goslings vs birth year of female. Same sample as in Figs 29-32.
Antal hunner, der producerede mindst én unge (sort), og hunner, der ingen unger producerede i deres levetid, afsat mod hunnernes fødselsår. Der er ikke de store forskelle mellem de forskellige årgange af hunner, bortset fra at hunner fra 1965-1969 havde ringe succes (G_1 = 8,00, P = 0,005; hver af de to årsgrupper homogene: 1965-1969 G_4 = 2,57, P = 0,63; øvrige år G_{10} = 8,12, P = 0,62; år med tre eller færre hunner udeladt). Samme hunner som i Fig. 29-32.



Discussion

From its outset in 1959 the Greylag Goose project at Utterslev Mose evolved to some extent, with the major changes occurring in 1966-1968. From that time onwards, sexing and weighing of goslings were standard procedures, as was the assignment of goslings to broods so that their parents' identity was recorded, and the history (size, adoption) of the brood in which they grew up was known. During the same time, the geese gradually grew very tame, which probably implied that the record of present birds became more complete.

The goose population increased slowly during the sixties, and more rapidly after temporary setbacks in the early seventies and the early eighties, so that the population by the end of the study was almost three times as large as in the mid-sixties. There is little indication, however, that the results were much affected by density dependent factors. Variables being influenced by the population size should change over time as well, but apart from an increasing survival, apparently related to a decreasing shooting intensity, only minor trends were suggested in the analysis. The occurrence of adoption may have increased somewhat in parallel to bird numbers, and there was some evidence that emigration rates of male goslings increased. In conclusion, the records appear to represent a fairly homogeneous time series with little systematic change over the years.

Below, the magnitudes and interrelationships of the various fitness components of Greylag Geese at Utterslev Mose are summarised and commented upon in the light of results from other studies, of Greylag Geese and other goose species. Along the *r*-*K* continuum of life-history types in birds (e.g., Newton 1998), geese hold an intermediate position. They are fairly long-lived, although survival rates do not attain the extreme levels found in, e.g., many seabirds. They defer breeding at least to the age of two years, and on average for one or two years more. And they produce a single, but fairly large brood per season. Their populations should thus be able to withstand a rather high level of added mortality (shooting) before starting to decline, and to recover rapidly after natural disasters or periods of overexploitation. This is borne out by the history of many goose populations in Europe and North America (Madsen et al. 1996, 1999).

Among geese, the Greylag Goose seems to be characterised by having a slightly more *r*-type life-history than arctic-breeding species and populations, laying a larger clutch and fledging more goslings. Most likely, this tendency is largely the result of the more benign breeding environment of the Greylag Goose, the less restricted breeding period, and the shorter distances between staging/ feeding sites and the breeding grounds.

Annual survival

Return rates indicated that an average of 55-60% of the female goslings survived their first winter. Return rates of males were lower, evidently because a significant proportion emigrated to other sites, although a slightly lower survival of young males than of young females remains a possibility – it was suggested by maximum likelihood estimates but could have been an effect of a mismatch between model and data.

In both sexes, first-year survival varied considerably from year to year. An increasing tendency over time could be confirmed for the females, but not for the males, perhaps because it was masked by an increasing tendency to emigrate. Hunting appears to be a major mortality factor, and annual hunting levels and mortality rates are well correlated.

In Scania, Sweden, gosling survival between fledging and 1 July the following year was considerably better than in Utterslev Mose, 0.75 or more in most years (Nilsson et al. 1997), whereas prefledging survival of goslings was much poorer than apparent at Utterslev Mose (0.64 vs c. 0.9). Intensive shooting in Denmark may partly explain the difference in post-fledging survival, but it may also be that the benign conditions at Utterslev Mose permit the survival and fledging of some goslings that are too weak to make it until the following year. The combined survival, from hatching until the next season, appears not to be very different between the two study areas.

For adults ringed as goslings and more than four years old, the annual survival was about 0.80 towards the end of the study period. At least for females, it increased during the period, so the average value was lower, c. 0.74, significantly less than the average value for females ringed as adults (0.82). From recoveries of geese ringed at various moulting sites in Denmark, most of them at Vejlerne in northern Jutland, Paludan (1973) estimated the survival of adults in the 1960s at 0.68.

The fact that survival estimates based on adult-ringed birds were higher than the estimates based on gosling-ringed geese 5 years or older is noteworthy, although the difference was significant only for the females. Differences between these samples were also seen in fecundity components, generally so that adult-ringed birds did better than those ringed as goslings. The reason is not known, but the observation may serve as a warning, telling us that 'old' chicks are not necessarily equivalent to adults in bird-ringing analyses. Kampp (1991) reached a similar conclusion for Brünnich's Guillemot *Uria lomvia* and suggested that samples of adult-ringed birds might often be biased in favour of high 'quality' birds.

The average survival rate of adult Utterslev Mose geese was of similar magnitude to, or slightly less than estimates for other hunted populations where more or less direct evidence exists that hunting has a significant impact on population dynamics (which do not necessarily mean that they were overexploited): Greenland White-fronted Goose *Anser albifrons flavirostris* (Bell et al. 1993, Fox 2003), Lesser Snow Goose (Francis et al. 1992), Greater Snow Goose *A. caerulescens atlanticus* (Gauthier et al. 2001, Menu et al. 2002), and other populations summarised in Madsen et al. (1999). In Svalbard Barnacle Geese, on the other hand, which are fully protected throughout their range and annual cycle, about 90% of the adults survive from one year to the next (Bell et al. 1993, Owen 1984), and survival is also high in Svalbard Brent Geese *Branta bernicla hrota* (mean 0.87, Clausen et al. 1998). First-year survival appears to be much more variable than adult survival, both between years and between populations, but few good estimates exist. Utterslev Mose geese seem to enjoy a considerably higher first-year survival than Greater Snow Geese (estimated at 0.36 ± 0.12, Menu et al. 2002) and Lesser Snow Geese (0.42, Cooke et al. 1995). At the opposite end of the spectrum, first-year Svalbard Barnacle Geese may survive particularly well – data in Owen (1984) give a mean of 0.85 for 1975-1980, but that was measured from October, after arrival at the wintering grounds.

The proportion of UM adults reported shot among those assumed dead between one year and the next was high (about 30%), approximately the same as for first-year birds. This suggests that shooting was a major mortality factor even in adults. However, that does not necessarily imply that mortality rates were elevated because of hunting – although the observed increase in survival rates and decrease in recovery rates during the study period suggest that they were – or that hunting was overexploiting the population. After all, the population was growing during most of the study period. In a likewise growing population of Lesser Snow Geese, Cooke et al. (1995) concluded that hunting contributed little to the annual variation in mortality of first-year birds, but that the survival of adults had improved because a smaller proportion were shot. Similarly increasing survival rates have been found in most West Palearctic goose populations, and it is generally believed that a reduced hunting pressure was an important factor behind the impressive growth in these populations during the last decades of the 20th century (Ebbinge 1991, Owen & Black 1991, Madsen et al. 1999).

About two thirds of the recovered UM geese were shot in Denmark, with no apparent tendency over the study period (Fig. 5). About 20% were recovered in Spain, and almost all the rest in Netherlands and France (France showing a conspicuous increase during the last 5-year period). The recoveries reported by Paludan (1973) showed a somewhat different pattern in that only 46% came from Denmark and more than 10% from countries showing that the birds belonged to the Central European Flyway, most likely because Paludan's geese were ringed when moulting and thus of mixed origin.

In a study of neck-collared Greylag Geese breeding in Scania, southern Sweden, Nilsson & Persson (1993, 1996) noticed a markedly higher survival rate of birds wintering in the Netherlands than of birds wintering in Spain, and suggested that this difference was caused by a higher rate of shooting and shooting-associated disturbance experienced by the latter group in Spain and France. Unfortunately, apart from the recoveries no information on wintering habits of individual birds is available for the Utterslev Mose geese, so it is not possible to investigate if they exhibit a similar difference in survival dependent on winter quarter, or if it is masked by the intensive shooting in Denmark. The Greylag Geese in Scania pass the easternmost parts of Denmark only (Andersson et al. 2001) and thus to a large extent escape hunting here.

Natal and breeding philopatry

Roughly 8% of the surviving Utterslev Mose females and 45% of the males appeared to emigrate and settle at some site other than Utterslev Mose, but for females the estimate was probably inflated – perhaps grossly so – owing to the fact that about 10% of the goslings were erroneously sexed at ringing, and that a much higher proportion of missexed 'females' could be expected in the subsample of emigrated birds. In southern Sweden, 13% of females settled at other lakes than where they were reared, while 82% of males did so (Nilsson & Persson 2001a). Even when allowing for some problems of definition – the distance between the natal lake and the lake where recruited was sometimes smaller than the 3 km SW-NE extension of Utterslev Mose – these emigration rates appear to be considerably higher than those of the Utterslev Mose geese. However, emigration rates in Sweden depended on the natal lake; of males from the lake offering the best feeding conditions only 64% emigrated. If such a pattern is general in Greylag Geese, the low emigration rates suggest that Utterslev Mose is a prime habitat for breeding geese, a supposition confirmed by the high and increasing density of pairs and the apparently very high survival of goslings.

In Utterslev Mose, as well as the Swedish study area (Nilsson & Persson 2001a), adult males, like females, exhibited a strong philopatry to their breeding area, also after remating.

Reproduction

At a first glance, the Utterslev Mose dataset here analysed appears to be ideally suited for estimating parameters relating to fecundity and breeding propensity components of a life-cycle model (cf. Cooke et al. 1995). The study period extended over about two maximum life spans of the birds, and for the females the population is almost closed. However, the limitations of the data should not be ignored. There is no direct information on nesting, hence no data on clutch size or egg survival, or on intra-specific nest parasitism. Also, some breeding attempts failing at an early stage probably went undetected, and even the successful hatching of some pairs loosing their goslings soon after hatching appears to have been overlooked. Furthermore, the prevalence of brood amalgamation and adoption renders the production of fledglings by most pairs somewhat uncertain. To this comes the previously mentioned problems with sexing and the consequent bias in favour of long-lived birds in subsamples of sexed geese. Comparisons over age were generally based on sexed birds, implying that contributions by the youngest age-classes are likely to be underestimated, particularly in case of 'negative' characteristics (not mating, not breeding).

A further concern when comparing age-classes is that all included birds should have a non-zero probability of contributing throughout the range of ages considered. In case of attainment of breeding status, for example, it turns out that only cohorts born in 1983 or earlier should be included, and where the entire life span of the birds is considered the sample should be further limited to those born in 1981 or earlier. It could be argued, of course, that very old novice breeders or very long-lived birds are so few that the error caused by increasing the samples with a few more cohorts would do little harm. The choice would necessarily be somewhat arbitrary, however, and since it would not change the results much it was here decided to keep with the samples as stated above.

A small proportion of the geese at Utterslev Mose bred when 2 years old, some of them successfully, but the majority postponed breeding until one or a few years older. Breeding propensity increased until the age of about six years, after which the geese bred in four years out of five. The brood size (as recorded a couple of days after hatching) varied with the age of the mother and whether the brood was or was not later enlarged by adopted goslings (Table 12), but the overall mean was about 4.8 goslings. The nest success (percent of nests that hatched at least one gosling) was about 60% overall, but 72% for females aged six years or more, and 76% for females ringed as adults. Corresponding figures for apparent brood success (percent of broods yielding at least one fledgling) were 84%, 85% and 90%, respectively, but the widespread occurrence of adoption means that these percentages say little about true success and brood survival. Apparent gosling survival – total number fledged relative to total number hatched – was very high, about 91%.

The larger initial size of broods of parents that subsequently adopted additional goslings stands in contrast to the report of Williams (1994) who found no such difference in a population of Lesser Snow Geese. Some of the broods later receiving adopted goslings at Utterslev Mose may have been enlarged already when discovered, but this certainly does not explain all the difference. It seems that parents producing large broods are also prone to adopt goslings, both probably being associated with general fitness and dominance status of the parents.

Jørgensen (1986) reported on brood sizes of Greylag Geese at various sites in Denmark during 1970-1985, mainly in southern Zealand and the island of Lolland. The overall mean of 1567 broods was 5.31 goslings, a little more on Lolland (5.52, n = 758) than on Zealand (5.11, n = 809), and broods were generally larger during 1976-1982 than in other years. The age of the broods at counting varied but was generally less than one month. The nest success during 1972-1978 of 285 pairs at four undisturbed sites was estimated at 73 %. Both brood size and nest success appear to have been slightly higher than at Utterslev Mose, but since nothing is known of the age distribution of the parents or the occurrence of adoption it is difficult to compare the results from the two studies.

The study in south Sweden of neck-collared Greylag Geese have produced results largely in accordance with those from Utterslev Mose as regards brood size and nest success, and the effect of parent age (Nilsson & Persson 1994). Of the experienced pairs, 65% produced a brood during 1985-1992, the mean size of the broods being 4.74 (4.60 for all pairs). However, fledging success appears to have been much poorer in south Sweden than at

Incubating goose, Utterslev Mose 21 April 1991. Photo: Ole Banke.

Utterslev Mose, about 69%, whereas brood success was about the same (89%). Adoption was relatively infrequent in the Swedish study (Nilsson & Kampe-Persson 2003), and the high brood success, in spite of the relatively high mortality rate of goslings, apparently arose in a slightly different way than the similar value at Utterslev Mose; in Sweden the pairs retained their relatively few surviving young, at Utterslev Mose few goslings died but some pairs lost their brood to other pairs.

Greylag Geese tend to lay larger clutches than most other goose species (Cramp & Simmons 1977), and so to hatch larger broods, especially when compared with arctic-nesting species. The mean brood size of Lesser Snow Geese was 3.6 (Cooke et al. 1995), and of Greenland White-fronted Geese 4.0 (average over two years, Fox & Stroud 1988); Baltic Barnacle Geese hatched 3.3 goslings per brood over 9 years (Larsson & Forslund 1994).

Concerning lifetime reproductive success (LRS), the results from Utterslev Mose fit well into the general synthesis given by I. Newton, derived from the contributions in the volume he edited and covering a wide variety of bird species (Newton 1989). The main generalisation is the great variation between individuals: a large proportion of produced fledglings (42-86% in the included studies vs 45-50% at UM females) die before they can breed, not all that survive that long do produce fledglings (51-98% vs 52% in Fig. 29) or even attempt to breed, and the production of successful individuals varies greatly (15-30% of productive individuals producing 50% of the offspring compared to 17% in Fig. 30). Percentage of variation in LRS of birds surviving to breeding age that was accounted for by variation in life span varied between 6-66% in the studies in Newton (1989); in Utterslev Mose females it was 60%.

Values from Utterslev Mose are not strictly comparable to those reported in most of the other studies because production was based on hatched young, not fledglings. In the study of Barnacle Geese (M. Owen & J.M. Black, in Newton 1989) the basis was juveniles in family flocks after arrival to the wintering grounds.

Factors affecting breeding performance and gosling survival

Age appears to be a major determinant of breeding performance in Greylag Geese. In the Utterslev Mose population, breeding propensity, nest success and brood size all increased with age, in the case of breeding propensity until the geese were 6-7 years old. Apparent survival of post-fledging goslings also increased with parent age, although the relationship was not particularly strong. For some parameters a decreasing performance of the oldest geese was suggested, but the sample of birds more than 10 years old was small. Similar age effects have been reported from many studies covering a wide variety of species (e.g., most chapters in Clutton-Brock 1988 and Newton 1989). A significant increase of almost all components of reproductive performance has been found in Lesser Snow Geese (Rockwell et al. 1993) and Barnacle Geese (Owen 1984, Black & Owen 1995), both species reaching peak performance at an age of about six years and showing some decline in older breeders, after about the 7th and 11th year, respectively. For Greylag Geese in southern Sweden, the mean brood size increased with parent age until four years (Nilsson 1998), as was the case at Utterslev Mose.

The mating system in geese is characterised by strong, monogamous pair-bonds commonly lasting for the lifetime of the mates. This suggests that long-term monogamy is selectively advantageous, so that some penalty of changing mate would be expected, at least in the short term. In the present study, females remating after being widowed or divorced abstained from breeding more often than females mated to the male of the previous year, and a slight effect on the success of those that attempted to breed was also apparent in the subsample ringed as goslings. Brood size showed a non-significant decrease in females with new mates, who were also less prone to adopt goslings. In all respects, however, remating experienced breeders did better than first-time breeders.

No difference in performance could be detected between females remating because the former partner was dead and those that had been divorced, except that the few adult-ringed females that became divorced were particularly liable to refrain from breeding. However, the data were too sparse for a meaningful discussion in terms of general hypotheses on divorce in normally monogamous species (cf. Ens et al. 1993, Black 1996). In their study population in Sweden, Nilsson & Persson

(2001b) found some support for the *better option hypothesis*, according to which divorce occurs because one member of the pair has the opportunity to acquire a better quality mate and thus improve its reproductive success. However, the authors also stressed that divorce occurred for a variety of causes. In hunted species, like the Greylag Goose, an obvious possibility is that one pair member has been wounded. Madsen & Noer (1996) showed that Pink-footed Geese *Anser brachyrhynchus* carrying shotgun pellets had lower survival than non-carriers, suggesting a reduced general body condition that might also afflict the bird's performance as a breeder. Divorce following a reduction in fitness of one mate, from whatever reason, could be viewed as a special case of choosing the better option on the part of the other member of the pair.

Many studies have shown a relationship between timing and success of breeding in various species of birds, most often so that early breeders do better than late breeders (cf. review by Daan et al. 1988). In the present study, a connection was evident between hatching date and number of goslings (initial brood size), and goslings from early broods had higher post-fledging survival. However, age and timing of breeding were interrelated, with older breeders laying earlier than younger breeders, and much of the apparent effect of laying date seemed actually to be an effect of parent age.

Body mass may be assumed to be related to nutrient reserves and general body condition and health (and competitive ability), so it would be expected that heavy fledglings survive better than light fledglings. It is therefore not surprising that studies have often demonstrated such a relationship (e.g., Cooke et al. 1995), although exceptions occur (Hedgren 1981, and references therein). In the UM geese, body mass of goslings at ringing did appear to affect post-fledging survival of female goslings, the two being positively correlated, but again, body mass of goslings and parent age was correlated (while a negative relationship existed between body mass and laying date). Nilsson et al. (1997) found similar effects of hatching date and gosling weight as here reported. The relationship between gosling weight and parent age was complicated by the widespread occurrence of adoption in Utterslev Mose, because goslings in broods containing many adopted young tended to be light, and such broods were slightly more common in the sample of older parents.

In male goslings, the relationship between body mass and apparent survival (return rate) was puzzling in that it tended to be negative. Combined with the relatively large mean weight of male goslings in the Rest group, which consisted of a mixture of birds that died during their first year of life and birds that emigrated from Utterslev Mose, this suggests that heavy male goslings were particularly prone to emigrate. The same was found in a study of Barnacle Geese by van der Jeugd (2001) whose explanation was that heavy males were better able to overcome the difficulties of establishing in an unfamiliar area. However, since large males were also at a competitive advantage in their natal colony, and apparently did not benefit from their choice to disperse, this explanation is incomplete. One possibility is that males disperse in order to reduce the risk of mating with a close relative (H. Kampe-Persson in litt.). Sex-biased natal dispersal is often viewed as a behaviour evolved as a mechanism for avoiding inbreeding, although other benefits are possible and in some cases more important (Ralls et al. 1986). Be that as it might, males probably tend to emigrate because they sometimes benefit from it, or have benefited from it in their evolutionary past.

The factors that influenced survival of the goslings seemed to have little significance for the female survivors' chance of becoming breeders (Table 25). No statistically significant effects on recruitment probability were apparent of laying date of brood, parent age, or brood size, although a disadvantage was suggested of having belonged to a brood with adopted goslings, and of having a young and late-laying mother. In addition, heavy females had a better chance of recruiting than other females (Table 26). In Scania, southern Sweden, Nilsson et al. (1997) found an even stronger relationship between gosling weight and recruitment rate.

Adoption

Adoption has been widely reported in geese (Ramsey 1951, Raveling 1970, Prevett & MacInnes 1980, Zicus 1981, Lamprecht 1986, Cooch et al. 1991, Persson 2002) and was reviewed by Eadie et al. (1988), who preferred the term post-hatch brood amalgamation (pre-hatch brood amalgamation being their term for intra-specific nest parasitism).

In Utterslev Mose as many as 18-28% of the pairs enlarged their broods by adopting goslings. The exact proportion depends on the true status of broods assigned an adoption score of 1, and since these broods in most respects appear to group with those that certainly received adopted goslings, the proportion cannot have been much below 25%. This is a much higher occurrence of adoption than reported from other localities (cf. Kampe-Persson 2002). However, it agrees fairly well with results from studies using genetic techniques (Svalbard Barnacle Geese 16%, Choudhury et al. 1993; Baltic Barnacle Geese 27%, Larsson et al. 1995), and Williams (1994) found that 131 (13%) out of 982 families of Lesser Snow Geese adopted at least one young in a total of 146 events (15 pairs adopting twice).

However, in most reported cases the numbers of adopted goslings have been low compared to numbers observed at Utterslev Mose, so even if the phenomenon was probably overlooked in some previous studies of Greylag Geese, the occurrence of adoption at Utterslev Mose appears to be exceptional. This could simply be a result of the high density of grazing families on the lawns, combined with the rather narrow corridors to and from the water – most of the shoreline is reedbed or shrub, with only minor stretches where the lawns reach the water's edge. Details of events where goslings are transferred between families have never been described, however.

Adoption appears not to be caused solely by accidental mixing of broods, although Williams (1994) concluded that it was a passive process on the part of the adopting adults. Parent geese recognise their goslings 10-15 days after hatching (Ramsey 1951, Prevett & MacInnes 1980), and although adoption events mainly take place during the first few days, it may happen 4-12 weeks after hatching (Choudhury et al. 1993); in Williams' (1994) study of Lesser Snow Geese almost half of the events happened later than 15 days after hatching, and in Canada Geese *Branta canadensis* 35% occurred later than 35 days after (Zicus 1981).

This raises the question why parent geese should accept foreign goslings. Costs associated with caring for additional young may be low in precocial birds (Pierotti 1988, 1991, Choudhury et al. 1993), and in geese a large family size appears directly to benefit its members. Larger broods have been found to grow faster than smaller broods (Cooch et al. 1991), and dominance rank and therefore access to the best feeding patches on wintering and spring staging grounds is associated with the size of the social group (Raveling 1970, Lamprecht 1986, Black & Owen 1989a, 1989b, Gregoire & Ankney 1990, Black et al. 1992).

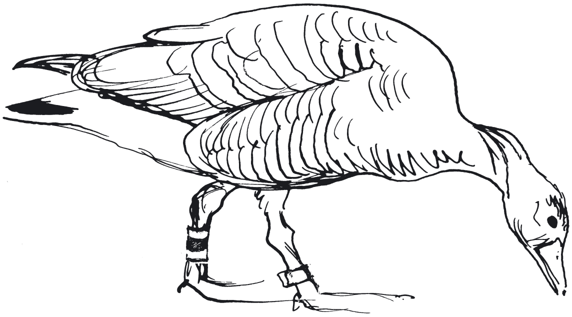
However, it has been difficult to demonstrate any benefit in terms of biological fitness, although Nilsson & Kampe-Persson (2003) did find that family size was positively related to gosling survival and recruitment. In Svalbard Barnacle Geese, Loonen et al. (1999) likewise found that the generally faster-growing goslings in large broods survived better, with no apparent net cost to the parents in survival or breeding performance the following year. Larsson et al. (1995), on the other hand, found no difference in post-fledging survival or age at first breeding between extra-pair goslings and intra-pairs goslings from broods with or without extra-pair brood mates and concluded that costs or benefits of adoption, if existing, were small. In the present study no benefits of adoption could be detected either, so if existing at all, such benefits may only become manifest in situations with strong intra-specific competition for food.

Population

The goose population of Utterslev Mose increased slowly during the sixties, and more rapidly after temporary setbacks in the early seventies and the early eighties, so that the population by the end of the study was almost three times as large as in the mid-sixties (Fig. 3).

The two depressions in the population curve were caused by factors operating for a short period only. Utterslev Mose was at its most polluted stage in the late 1960s, with several outbreaks of botulism among waterbirds, whereas geese, as might be expected, were apparently unaffected (Fjeldså 1973). Instead, the decline between 1971 and 1972 may have been a delayed effect of the severe and extended winter of 1969/70, where late ice cover of Utterslev Mose prompted some pairs to move 2 km to breed in (the partly ice-free) Kagsmosen (Jensen 1998). However, neither the proportion of females that bred nor the success of those who did were particularly low in 1970 or the following years, and generally the geese do not appear to be very sensitive to cold winters – three ice winters in succession (1984/85-1986/87) left no mark on the population curve. Also, a temporary exodus to Kagsmosen was noted even in 1971 and in the late 1960s (this study), but not in other years with late ice cover, suggesting that the cause was the generally deteriorated conditions at Utterslev Mose rather than ice cover in spring.

The decline in the early 1980s affected the entire west Baltic population and may with some reliability be ascribed to problems with the water regimen at the Guadalquivir Marismas during these winters, culminating with severe droughts in 1980-1983 (Fog 1981, Amat 1986, Madsen 1987). In dry conditions, the geese have difficulty obtaining sufficient food, meaning higher mortality and



poor condition when the survivors return to the breeding grounds. In addition, many geese are forced out of the Doñana National Park (where they have been protected since 1983/84) to surrounding areas where they are heavily shot; the same may happen in very wet winters with an extremely high water level (Nilsson & Persson 1996, Persson 1996). Return rates to Utterslev Mose in 1981 were low, and the proportion of females initiating breeding as well as breeding success were well below average in both 1980 and 1981.

Madsen (1987) doubted if the low mid-winter counts in 1980-1983 reflected a true population decline, suggesting instead that the geese had dispersed over wider areas and therefore had been more difficult to count. That the population decline was in fact real is strongly indicated in the data from Utterslev Mose, however. On the other hand, the low numbers at Utterslev Mose during the early seventies is not reflected in the mid-winter counts, confirming that this decline had its cause in local factors.

Before and between the two temporary population declines, the population grew slowly, apparently at a rate of roughly 2-3% per year. After the last setback, the population has grown by about 8% per year. Since the population appears to have been virtually closed (as far as the females are concerned), the growth during these subperiods shows that the population was not limited by density-dependent factors, in accordance with the lack of evidence of density-dependent variation in the parameters examined.

The increased growth rate during the last decade was probably a consequence of the decreasing mortality, which in adult females fell by 0.5-1% per year as an average. Other factors might have contributed, of course; but the change in survival actually has the right magnitude needed to produce the observed increase in growth rate. The decreasing mortality appears to have been a result of a gradually falling intensity of hunting.

Utterslev Mose as a breeding habitat for geese

The virtual absence of evidence of density-dependent effects on survival and breeding performance of the geese in Utterslev Mose despite the large and increasing population indicates that the park is able to support a very high number of birds, and that the population levels attained during the study were well below carrying capacity. Effectively, the carrying capacity may have increased early in the period, because the geese became habituated to humans and gradually began to graze farther and farther away from the water, in the end utilizing the entire area of lawns. But towards the end of the study many years later, at a considerably higher population level, Utterslev Mose evidently was still a prime habitat for geese, judged from very high pre-fledging survival of goslings and the weak effect of gosling weight on survival and recruitment. The high fidelity to the natal area (by goose stan-

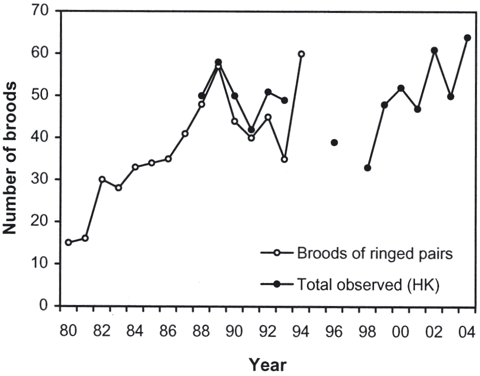


Fig. 34. Number of broods of goslings included in the database, 1980-1994 (ringed pairs), and total broods observed in UM after 1988 by Hanne Kapala (HK).
Antallet af kuld i databasen (ringmærkede par, åbne cirkler), og antal kuld i alt i UM optalt af Hanne Kapala (HK, fyldte cirkler).

dards) of Utterslev Mose males also suggests that conditions there were very good indeed, if the results of Nilsson & Persson (2001a) have general validity.

In this light it was unfortunate that the fieldwork was not continued a little longer. There is little information about the development of the population since 1994, but Hanne Kapala (in litt.) has counted the total number of broods in most years since 1988, and her figures are shown in Fig. 34 together with brood numbers from the database. It appears that there has been much variation since the late 1980s, but virtually no net increase. The suggestion is that already during the last years of the study the number of successfully breeding pairs reached a limit, so that a decreasing proportion of the growing population was able to hatch a brood. It would have been interesting to follow this development in detail and see how the values of the demographic parameters were adjusted. However, although it may never seem the right time to stop, even long-term studies have to end. And just as they are rarely planned at the outset, so the end can be sudden and unforeseen.

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During the study period, NOP received supplementary observations from UM and other sites from a number of people, of which the most persistent were Henning Jensen, Pelle Andersen Harild, Peter Hermansen, Hanne Kapala, Eddie Fritze and Kjeld Pedersen. Thanks also to the park administration of the Municipality of Copenhagen for permission to trap and ring the geese, and to the police of Copenhagen who always supervised our capture and ringing sessions and, if necessary, calmed down the spectators.

Photo: Ole Banke.

Resumé

Grågæssene i Utterslev Mose

Da Utterslev Mose i grænseområdet mellem Københavns og Gladsakse kommuner blev omdannet til et parkområde i 1939-1943, havde der allerede i mange år ynglet Grågæs *Anser anser* på lokaliteten, men kun i ringe tal. Bestanden begyndte langsomt at vokse i begyndelsen af 1950erne, og ved starten af det grågåseprojekt, der er emnet for denne afhandling, var der omkring 50 ynglende og ikke-ynglende par.

Starten på projektet var impulsiv og præget af tilfældigheder, og det stod bestemt ikke i kortene, at det skulle udvikle sig til et af de længstvarende arts-studier i Danmark – og i verden. I 1959 havde konservator Erik Petersen på Zoologisk Museum i København indgået en aftale med et københavnsk dagblad om at arrangere fugleture i Utterslev Mose, og i den forbindelse besluttede han sammen med en af forfatterne (NOP) at forsyne nogle af gæssene med genkendelige mærker, så turdeltagerne kunne se, at det var de samme fugle, der år efter år vendte tilbage til mosen. Samme år blev der derfor indfanget et beskedent antal gæs, som blev forsynet med såvel metalringe som farveringe.

I de følgende år blev mærkningen perfektioneret, idet alle indfangede gæs fik tre 10 mm høje, farvede plastikringe, der blev limet sammen til én 3 cm høj ring, samt en ligeledes 3 cm høj aluminiumsríng med 10 mm høje cifre, der var lette at aflæse. Desuden påbegyndte NOP systematiske iagttagelser af de tilstedeværende gæs. Blandt andet blev alle nyiagttagne individer hvert år nøje kontrolleret for at fastslå, at ringnummer og farvekombination passede sammen. Kun få individer mistede i årenes løb en eller flere farveringe, og i sådanne tilfælde blev ringnummeret kontrolleret så ofte som muligt. Fra 1965 blev der flere gange om ugen foretaget timelange observationer, der senere udviklede sig til næsten daglige iagttagelser af op til 5-7 timers varighed. Generelt blev hele området dækket fra cykel eller til fods.

Mærkningstallene er anført i Tabel 1. I løbet af ret få år bar en betydelig del af de tilstedeværende gæs i mosen ringe (Fig. 4). Det var især tilfældet med hunnerne, fordi næsten alle overlevende hunner klækket i mosen er vendt tilbage og har slået sig ned her som voksne, mens en del af hannerne er udvandret til andre lokaliteter. Samtidig er gåsebestanden i mosen vokset betydeligt (Fig. 3), i begyndelsen langsomt og med to tilbageslag, men fra 1983-84 til projektets afslutning i 1994 ganske hurtigt, med omkring 8% om året. Tilbagegangen i begyndelsen af 1970erne skyldtes tilsyneladende lokale forhold, mens tilbagegangen i begyndelsen af 1980erne gjaldt hele flyway-bestanden og hang sammen med forholdene i det vigtigste overvintringsområde, Doñana i Sydspanien.

Sigtet med projektet udvidedes hurtigt i forhold til det oprindelige ønske om at kunne demonstrere fuglenes stedtrohed, men det forblev ret vagt defineret. De indsamlede data var først og fremmest hvilke fugle der var set i mosen et givet år, men også deres køn, deres ynglemæssige status, identiteten af deres mage hvis denne var mærket, samt størrelsen af et evt. kuld til at begynde med og gennem ungetiden. Fænologiske data som dato for ankomst og dato for klækningen af et evt. kuld indgik ligeledes, og fra sidst i 1960erne blev identiteten af de mærkede ungers forældre (eller adoptivforældre) noteret, ligesom ungerne blev vejet i forbindelse med ringmærkningen. I databasen indgik også oplysninger om genfund af de UM gæs, der var genmeldt som døde i Danmark og udlandet.

Projektet sluttede med sæsonen 1994, da NOP gik på pension. På det tidspunkt var data indtastet i en elektronisk database, men der var ingen bearbejdning foretaget, og der var en reel fare for at det aldrig ville ske, og at anstrengelserne havde været forgæves. Det var derfor meget glædeligt, at Aage V. Jensens fonde trådte til i 2002 og gjorde det økonomisk muligt for KK på fuld tid at hellige sig opgaven med at få databasen kvalitetssikret og dokumenteret samt at foretage den bearbejdning, der hermed foreligger i form af nærværende publikation. Her berøres de fleste spørgsmål, som data kan belyse, men hovedvægten ligger på populationsdynamiske parametre, altså størrelser som dødelighed og ungeproduktion for de forskellige aldersklasser, samt betydningen af en række forhold, der vides eller formodes at have indflydelse på disse parametre.

Fænologi og træk

De fleste danske Grågæs forlader landet om vinteren. Bestanden tilhører den vestbaltiske population, der primært overvintrer i Holland og Spanien. I alt er 1165 af projektets gæs blevet genmeldt frem til ynglesæsonen 1995, et år efter mærkningen af det sidste hold gæslinger. Heraf er 86% rapporteret skudt, en andel der ikke varierer væsentligt mellem fugle mindre end ét år gamle, ældre fugle mærket som unger, og fugle mærket som voksne. Med få undtagelser er fuglene skudt i Danmark, Holland, Frankrig eller Spanien (Fig. 5). Holland er relativt svagt repræsenteret, idet jagt på gæs her primært sker på dispensation for at beskytte afgrøder.

Ankomsttidspunktet til UM er vist i Fig. 6 for alle årene under ét. Gennemsnitsdatoer for de enkelte år er vist i Fig. 7. Ankomsten sker senere i kolde forår og er negativt korreleret med gennemsnitstemperaturen for marts. I gennemsnit ankommer de ældre fugle før de yngre, og forskellen mellem de tre yngste aldersklasser – og mellem disse og de 4-årige og ældre fugle – er signifikant (Tabel 2-3). Ynglefænologien er illustreret i Fig. 9 i form af gennemsnitlige klækningsdatoer for de enkelte år. Ligesom for ankomstdatoen er der en faldende – men ikke helt signifikant – tendens gennem undersøgelsesperioden.

Kønsbestemmelse af gæssene

Efter midten af 1960erne er de fleste mærkede gæslinger blevet kønsbestemt i forbindelse med ringmærkningen, og desuden er alle tilstedeværende voksne gæs hvert

Photo: Vibeke Tofte.

år så vidt muligt blevet kønsbestemt ud fra adfærd og udseende. For udparrede og især ynglende fugle indebærer dette ikke større problemer, men for enlige fugle har det ikke altid været muligt. Kønsbestemmelsen af gæslingerne er også behæftet med fejl, og ca 10% af såvel hunnerne som hannerne i UM er tilsyneladende blevet fejlbestemt (Tabel 6).

Når usikkerheden i kønsbestemmelsen er værd at fremhæve, skyldes det at den kan få mærkbare konsekvenser i forskellige analyser, fordi kønnene "opfører" sig forskelligt. For eksempel slår næsten alle hunnerne sig ned i UM, mens mange hanner udvandrer. Derfor er de fejlbestemte "hanner" – som altså i virkeligheden er hunner – meget mere tilbøjelige til at komme tilbage til mosen end de korrekt bestemte hanner, så sandsynligheden for at en tilfældigt valgt "han" i mosen var fejlbestemt er næsten 20%, mens kun ca 5% af de tilbagevendte "hunner" i virkeligheden var hanner (Tabel 6). Omvendt vil de fejlbestemte "hunner" være overrepræsenteret blandt de emigrerede fugle (som bare ikke kan kontrolleres efterfølgende), og højst tænkeligt har flertallet af de emigrerede "hunner" – typisk genmeldte fugle oprindeligt noteret som hunner, men ikke siden set – i virkeligheden været hanner.

Reelt er kønnet således kun kendt med sikkerhed for en fugl, hvis den er set som voksen i mosen, specielt hvis den har været udparret og opført sig rimelig "typisk". En konsekvens er, at hvis man estimerer dødeligheden for de sikre hanner og hunner, fås en *mindre* dødelighed hos de et-årige end hos de ældre fugle, simpelt hen fordi stikprøven har overvægt af relativt længe-levende fugle – og specielt et underskud af fugle, der kun optrådte i mosen som et-årige.

Retur-rater og overlevelse

Den årlige overlevelse – og dermed dødeligheden – beregnes ud fra antallet af fugle, der vides at overleve frem til den efterfølgende sæson, enten fordi de her (eller senere) ses i UM eller andetsteds, eller genmeldes som nyligt døde. Det betyder, at gæs, der udvandrer til andre ynglelokaliteter, bliver betragtet som døde, med mindre de senere genmeldes. Emigration og dødelighed kan derfor ikke klart adskilles. Der findes ganske sofistikerede modeller, fx implementeret i software-pakken MARK, som tillader estimering både af emigrationsrate og mortalitet, men modellen passer ret dårligt til virkeligheden for gæssene i UM; bl.a. opererer modellen kun med permanent emigration, mens mange af mosens gæs er udeblevet et enkelt eller nogle få år, især i deres unge år (jf. Fig. 2 og Tabel 8). Desuden er emigranter undertiden vendt tilbage til UM. Dertil kommer problemerne med kønsbestemmelsen.

For første leveår er i stedet beregnet "retur-rater" som simple forhold mellem antal overlevende og antal mærkede, og for ældre årgange som forholdet mellem antal overlevende og antal i live i udgangsåret. For førsteårsfuglene ses resultatet for tre delperioder og for alle år under ét i Tabel 9, mens den årlige variation er afbildet i Fig. 10. Der er en betydelig årlig variation, som til dels utvivlsomt er reel, men som også afspejler det lave antal mærkede gæslinger i visse år, og de antydede tendenser – stigende for hunner, faldende for hanner – er ikke signifikante. Samme tendenser ses imidlertid også i Tabel 9, og den forstærkes når der korrigeres for fejlagtig kønsbestemmelse af gæslingerne (yderste højre søjle). For hunnerne udgør retur-raten utvivlsomt et godt estimat af overlevelsen, og denne er således vokset gennem undersøgelsesperioden; for hannerne har overlevelsen sandsynligvis været omtrent den samme som for hunnerne, men en ret betydelig og åbenbart stigende andel er udvandret.

For ældre fugle ser det ud til, at retur-raterne nøje afspejler overlevelsen, også hos hannerne. De fundne værdier er vist i Fig. 11 for alle år under ét, mens den årlige variation for fugle mindst 5 år gamle (eller mærket som voksne) er afbildet i Fig. 12 (13). Ligesom for ungfuglene er denne variation ganske stor, hvilket også her til dels må skyldes tilfældigheder, men også i nogen grad afspejler virkelige forskelle i overlevelsen; fx stemmer den lave retur-rate i 1981 med tilbagegangen i bestanden dette år, og med rapporterne om forholdene i overvintringsområdet Doñana i Spanien.

De adult-mærkede ser i øvrigt ud til at overleve bedre end de unge-mærkede, også selv om kun ældre unge-mærkede betragtes (≥5 år gamle), se Tabel 10. Forskellen er signifikant for hunnerne og advarer om, at ældre unge-mærkede ikke nødvendigvis er ækvivalente med adult-mærkede, når det gælder ringmærkningsanalyser. Vi skal senere se, at adult-mærkede hunner i gennemsnit også producerede flere unger end hunner mærkede som unger.

Endelig kan det anføres, at hunner overlevede lidt dårligere, når de fik flyvefærdige unger, end når ikke gjorde; forskellen var dog ikke signifikant (Tabel 11). For hanner gjorde det omvendte sig gældende, og her var forskellen signifikant for de adult-mærkede. Der er ingen umiddelbar forklaring på forholdet, og det er heller ikke klart hvad der er årsag og hvad der er virkning i denne sammenhæng.

En stor del af de døde gæs blev åbenbart skudt. For førsteårsfuglene udgør genmeldingsraten – antal genmeldte i forhold til antal mærkede – et minimumsestimat af jagtdødeligheden, såfremt kun genmeldinger af skudte fugle medtages. Genmeldingsraten er aftaget gennem årene, fra godt 18% i 1966/67 til knap 7% i 1994/95 (Fig. 14). Til sammenligning synes dødeligheden at være faldet fra ca 50% til ca 36% (Tabel 9), altså betydeligt højere tal end den kendte jagtdødelighed. Men al erfaring siger, at kun en del af de fundne ringe rapporteres, så den ikke-kendte del af jagtdødeligheden er formentlig af samme størrelsesorden som den kendte. Samtidig er der en klar korrelation mellem årlige genmeldingsrater og andelen af hunner, der ikke er returneret ($r = 0,445$, $P = 0,02$), så jagt synes at have været en væsentlig dødelighedsfaktor. For de ældre fugle synes genmeldingsraterne at have været ca halvt så store som for ungfuglene (de kan ikke beregnes direkte), og da dødeligheden rundt regnet også har været halvt så stor som for førsteårsfuglene, må jagt have været en lige så stor dødelighedsfaktor for de ældre fugle. De faldende genmeldingsrater afspejler utvivlsomt et reelt faldende jagttryk, og i overensstemmelse med det er gæssenes årlige overlevelse vokset gennem perioden.

Reproduktion

Grågæs yngler tidligst som 2-årige, men oftest starter de noget senere. For hunner var gennemsnitsalderen for første pardannelse 1,9 år, for første yngleforsøg 3,3 år, for første klækning af et kuld 4,2 år, og for første vellykkede yngleforsøg 4,5 år (Fig. 16); for hanner var de tilsvarende tal 1,8, 3,5, 4,4 og 4,7 år, og statistisk set var der ingen forskel. Nogle gæs starter meget sent; fx ynglede hunnen #7601 første gang (uden held) som 5-årig og fik kun flyvefærdige unger i de to sidste af sine 10 leveår. En anden hun, #7108, var udparret hvert år fra hun var to år gammel til hun sidst blev set som 8-årig, men ynglede kun i de tre sidste år, hver gang uden held. Hannen #3349 ynglede ikke før han var seks år gammel, og blev først far til et klækket kuld to år senere; alligevel nåede han at få tre kuld flyvefærdige gæslinger i sit 10 år lange liv.

I gennemsnit dannede Grågæssene par med jævnaldrende partnere (241 nydannede par med kendt alder hos begge mager: $r = 0,655$, $P = 10^{-30}$). I gennemsnit ynglede parrene ikke hvert år; de mest faste ynglefugle var de ældre (≥6 år), hvor 70-80% ynglede i ethvert givet år (Fig. 18-19).

Hos ældre fugle mislykkes mellem en fjerdedel og en tredjedel af alle yngleforsøg før klækningen, mens klækningssuccesen hos yngre fugle er endnu lavere (Fig. 18). Især lykkedes meget få yngleforsøg i 1980-1981 (Fig. 20), hvor bestanden gik tilbage åbenbart som følge af dårlige forhold i vinterkvarteret, og det er nærliggende at antage, at mange hunner disse år vendte tilbage med utilstrækkelige næringsreserver. Der er også nogle par, der klækker et kuld men mister alle ungerne; men hos sådanne par er yngleforsøget ikke nødvendigvis mislykket, for tab af unger skyldes meget ofte, at disse er overtaget ("adopteret") af et andet par (se senere). Af samme grund kan der ikke siges noget præcist om ungernes overlevelse frem til ringmærkningen. Men ved at summere slut-størrelsen af alle kuld og dividere med den tilsvarende summerede start-størrelse fås indtryk af en meget høj overlevelse, ca 91% (Fig. 22). Enkelte år er slut-tallet imidlertid større end start-tallet, og selv om det ikke er naturstridigt (der kunne have været en netto-tilgang af unger fra umærkede til mærkede par), er det sandsynligt, at enkelte kuld i visse år ikke blev opdaget før de blev forenet med et andet kuld og overtaget af dette kulds forældre. I så fald er den reelle ungeoverlevelse lidt mindre end de anførte 91%.

Størrelsen af ungekuldene kort efter klækningen varierede fra år til år, men der var ingen tendens (Fig. 21). Under ét var størrelsen af 829 kuld 4,80, lidt større (5,32) for kuld af adult-mærkede hunner og lidt mindre (4,55) for unge-mærkede hunner (Tabel 12). Som det ses afhang kuldstørrelsen tilsyneladende også af, om kuldet var tidligt eller sent (klækket før eller efter gennemsnitsdatoen for året), af moderens alder, og af om kuldet senere optog adopterede gæslinger. Gennemsnittet for de tidlige kuld var 5,11, for de sene kuld 4,55 ($P = 0.0015$), men det synes hovedsageligt at bero på, at ældre fugle yngler tidligere end yngre fugle; inden for aldersklasserne var forskellene ret små, og sene kuld havde ikke altid en mindre gennemsnitsstørrelse end tidlige kuld. Spredningen var også ganske stor inden for aldersklasserne, hvorfor mange af de tilsyneladende forskelle betinget af hunnens alder ikke er signifikante. Men de 2-3-årige hunner (der næsten alle ynglede for første gang) havde signifikant mindre kuld (3,82) end de hunner, der var fem år gamle eller ældre (4,38; stikprøven af kuld uden senere adoption, P = 0,043).

Det forhold, at kuld der senere fik tilført adopterede gæslinger var større end kuld, der ikke gjorde det, hænger formentlig sammen med, at socialt dominante par både får større kuld og er mere tilbøjelige til at adoptere fremmede gæslinger end subdominante par. Men da dominante par kan overtage unger fra andre par gentagne gange, kan det ikke udelukkes, at det for nogle af dem allerede var sket, da deres kuld første gang blev registreret (jf. ovenfor). Dette kan have bidraget til, at disse kuld i gennemsnit var større end andre kuld.

Adoption

Det er velkendt at Grågæs ofte "adopterer" fremmede gæslinger, dvs. overtager gæslinger fra andre par. Oftest er de adopterede gæslinger af nogenlunde samme alder som parrets egne gæslinger, så det ikke er muligt at skelne mellem dem. I UM materialet er alle unger henført til det par, der tog sig af "kuldet", uanset om dette rummede adopterede unger.

Adoption forekommer meget hyppigere blandt gæssene i UM end i andre undersøgte områder. Det hænger givetvis sammen med den store bestandstæthed og det forhold, at plænerne i mosen kun når ned til vandet på begrænsede strækninger. Hvis gæssene skræmmes, fx af fodboldspillere eller løsgående hunde, søger de mod vandet, hvorfor kuldene let bliver blandet ved sådanne lejligheder. Selv uden forstyrrelser kan det givetvis ske, at et dominant par jager et andet par væk fra et sådant område, og at de fordrevne ikke når at få deres unger med sig, eller ikke får lov til det.

Ud fra, at Grågæs kan lægge op til 12 æg, men tilsyneladende ikke effektivt kan ruge mere end 10, skulle 11-12 gæslinger i et kuld tyde stærkt på, at adoption havde fundet sted, og flere end 12 gæslinger skulle helt sikkert betyde, at kuldet var sammensat af gæslinger med forskellige mødre. I UM materialet kendes derudover kuldenes historie, så det vides om de på noget tidspunkt er blevet større. Der har derfor kunnet skelnes mellem kuld uden tegn på adoption; kuld der sandsynligvis rummede adopterede gæslinger (størrelse 11-12 og/eller med en tilvækst på 1-2 gæslinger på et eller andet tidspunkt); kuld der med sikkerhed havde adopterede gæslinger, men kun i moderat antal (størrelse 13-17 og/eller en tilvækst med 3-5); samt kuld med mange adopterede gæslinger (størrelse 18 eller derover, tilvækst med 6 eller mere). De to "sikre" adoptionskategorier er ofte slået sammen i det følgende.

Herudfra er adoption foregået gennem hele undersøgelsesperioden (Fig. 23). Hvis kuld med sandsynlig adoption lægges til dem med sikker adoption, har 28% af kuldene rummet adopterede gæslinger, og den stigende hyppighed gennem årene er signifikant (P = 0,02); hvis de i stedet lægges til dem uden adoption, var kun 16% af kuldene berørt, og tendensen var ikke signifikant (P = 0,09). Sandheden må ligge mellem disse yderpunkter, men der er forskellige indikationer på, at kuld med sandsynlig adoption i de fleste tilfælde faktisk var involveret i adoption.

Selv helt unge Grågæs kan adoptere fremmede gæslinger – i et tilfælde var hunnen blot to år gammel, mens hannens alder ikke var kendt. I alt var der 578 kuld, hvor hunnens alder var kendt, og 214 hvor hannens alder var; men kun 121 kuld, hvor alderen på begge forældre var kendt, 14 med sikker adoption og 91 uden tegn på adoption. Derfor er hunnens og hannens alder betragtet særskilt i Tabel 13. Det ses, at der er tegn på, at ældre fugle er mere tilbøjelige til at adoptere gæslinger end yngre fugle, men at forskellen kun er signifikant for hannernes vedkommende. Bemærk endvidere, at kuld med sandsynlig adoption i denne sammenhæng grupperer sig sammen med kuldene med sikker adoption.

Faktorer, der påvirker ungeproduktionen og afkommets overlevelse

Forældrenes overlevelse. Eftersom ungerne hos gæs forbliver sammen med forældrene frem til det efterfølgende forår, er det nærliggende at tro, at det forbedrer deres overlevelseschancer, og at bortfaldet af en eller begge forældre derfor vil reducere deres sandsynlighed for at overleve. Dette bekræftes af Tabel 14, men det ses samtidig, at ungernes overlevelse ikke er betinget af, at en eller begge forældre overlever. Bortfaldet af faderen synes at have større effekt end bortfaldet af moderen; ikke desto mindre overlevede 8 af 15 gæslinger (5 af 8 hunner) i et stort kuld, der mistede faderen allerede i maj, længe før gæslingerne var udvoksede.

Tab af forældrene har formodentlig størst betydning, når det sker tidligt. Kendskabet til hvornår forældrefuglene er omkommet er imidlertid begrænset til de relativt få tilfælde, hvor der foreligger en genmelding; ellers vides kun, at det er sket inden den følgende ynglesæson. Selv et tidligt tab af begge forældre udelukker dog ikke, at ungerne overlever – i et tilfælde overlevede en af to (hunlige) gæslinger i et kuld, hvis forældre begge blev skudt i september.

Mageskift. I betragtning af det stærke bånd, der tydeligvis er mellem magerne i et gåsepar, er det nærliggende at tro, at nyetablerede par har nedsat ynglesucces sammenlignet med par, der har holdt sammen i flere sæsoner. Det ser da også ud til at være tilfældet (Tabel 15-16). Især afstod nyetablerede par meget hyppigere fra at yngle end andre par, og hvis de ynglede lykkedes det sjældnere at klække et kuld. Nyetablerede mistede også deres unger hyppigere end andre par. Skønt alle fuglene i de her omtalte par havde været udparret også i det foregående år, var der en del ret unge fugle imellem (2-4 år), og effekten var særlig mærkbar hos disse unge gæs.

Hunner, der dannede par for første gang, er ikke betragtet i det foregående. Disse afstod næsten altid fra at yngle: af 634 par undlod 537 at yngle, 63 forsøgte men opgav før klækningen, og af de 34 par, der klækkede et kuld, mistede 13 deres unger. Det er en meget ringere succes end for andre unge-mærkede hunner i nyetablerede par.

De nyklækkede kuld var mindre hos nyetablerede par (4,78) end hos andre par (5,33), og mindst hos hunner, der aldrig før havde haft en mage (3,79). Den store spredning inden for hver gruppe gør dog, at forskellen kun er signifikant mellem de to ydergrupper.

De fleste mageskift skyldtes, at den tidligere mage var død, men især blandt de yngre hunner var der også en hel del "skilsmisser" (hvor den tidligere mage vides at have været i live; Tabel 17). Der var ingen afgørende forskel på mageskiftets effekt på ynglefrekvens og -succes mellem de to grupper, men det så ud til at skilsmisse påvirkede adult-mærkede hunner mere end unge-mærkede hunner.

Kuldets størrelse. Slutstørrelsen på ungekuldene er tæt forbundet med adoption (Fig. 23), så effekter af kuldstørrelse og adoption kan ikke adskilles i UM materialet. Men hvis det især er dominante par, der får store kuld og adopterer, burde ungerne i sådanne kuld have bedre chancer for at overleve, fordi de takket være (adoptiv) forældrenes status ville få adgang til de bedste fouragerings- og rasteområder. Subdominante gæs kunne i så fald ligefrem øge deres egen biologiske fitness ved at lade deres afkom blive overtaget af dominante par. Imidlertid er der intet i data, der tyder på nogen effekt af kuldstørrelse eller adoptionsgrad, hverken på ungernes overlevelse (retur-rate) eller deres chance for senere at etablere sig som ynglefugle (Tabel 20-22).

Forældrenes alder. Sammenhængen mellem hunnens alder og kuldstørrelsen er omtalt ovenfor. Betydningen af henholdsvis hunnens og hannens alder for ungernes overlevelse (retur-rate) synes at være ringe (Fig. 24), og en gruppering (2-5, 6-10, >10 år; Fig. 25) viste da heller ingen signifikans for hunnerne, men næsten for hannerne, takket være en høj retur-rate af unger af midaldrende hanner (6-10 år). Undersøgelsen blev gentaget med udelukkelse af årene 1989-1993 (Fig. 25), som på visse måder var atypiske, hvilket evt. også kunne berøre det diskuterede spørgsmål. I dette tilfælde var der en klar sammenhæng mellem førsteårsoverlevelsen af ungerne og såvel mødrenes som fædrenes alder. Afkom af unge forældre overlevede dårligere end unger af midaldrende forældre, mens billedet for unger af gamle forældre (over 10 år) var mere broget – unger af gamle mødre overlevede endnu bedre end unger af midaldrende mødre, mens unger af gamle fædre overlevede dårligere end unger af midaldrende fædre (men dog ikke så dårligt som unger af unge fædre).

Klækningstidspunkt. Hos fugle er det almindeligt, at tidlige kuld er større end sene kuld, og at ungerne fra dem også overlever bedre. Sammenhængen er ofte den, at ældre, erfarne fugle yngler tidligere end unge og uerfarne artsfæller, men en direkte fordel ved tidlig ynglen er heller ikke ualmindeligt – det må jo formodes at være grunden til de ældre fugles tidlige ynglen, mens yngre og mindre kompetente fugle er længere om at blive klar til yngletidens anstrengelser.

Størrelsen af ægkuldene kendes ikke for gæssene i UM, men størrelsen af de nyklækkede ungekuld aftog med 0,06 gæslinger pr dag, svarende til et fald fra 6,7 midt i april til 4,6 i sidste halvdel af maj (r = -0,57, P = 0,0004). Tilsyneladende falder ungeoverlevelsen frem til ringmærkningstidspunktet også med klækningsdatoen, men det afspejler primært, at tidlige kuld i højere grad end sene suppleres med adopterede unger. Adoption kan også sløre en eventuel sammenhæng mellem klækningsdato og førsteårsoverlevelse (retur-rate), fordi adopterede unger noteres med samme klækningstidspunkt som det kuld, de vokser op i. Som regel er forskellen dog lille, og der ses faktisk en klar sammenhæng mellem kuldets klækningsdato og retur-raten (Fig. 26).

Også for UM gæssene er det svært at skelne mellem en effekt af klækningstidpunkt og af forældrenes alder, fordi de ældre fugle også her yngler tidligere end de yngre. Indtil de er omkring 7 år gamle forskydes yngletidspunktet i gennemsnit med $2^1/_2$ dag for hvert år, fuglene bliver ældre. Herefter varierer yngletidspunktet uden nogen tendens.

Ungernes vægt. Det er nærliggende at antage, at tunge og velnærede unger overlever bedre end lettere unger. I materialet fra UM kendes vægten ved mærkningstidspunktet for en stor del af ungerne, men den kan ikke bruges direkte, da ungerne havde forskellig alder på det tidspunkt, og vægten i høj grad afspejler alderen og ikke ungens almindelige tilstand. I stedet er der set på vægtresidualer, dvs. vægtens afvigelse fra den "forventede" for den pågældende alder, nemlig den der findes på regressionslinjen vægt vs alder. Da hanner er tungere end hunner, er det gjort separat for hanner og hunner. Der kan ikke her korrigeres for fejl i kønsbestemmelsen, hvilket bidrager til den tilfældige variation i målingerne. Det samme gør adoption, som indebærer at nogle unger tillægges en lidt forkert alder; derfor er der nedenfor set både på den fulde stikprøve af vejede unger, og alene på de unger som stammede fra kuld uden tegn på adoption.

For hunner ses den forventede sammenhæng mellem større kropsvægt og bedre overlevelse, især når der ses bort fra kuld med adopterede gæslinger (Fig. 27). For hanner er billedet uklart i den fulde stikprøve, mens der ved frasortering af kuld berørt af adoption ses en signifikant *omvendt* sammenhæng. Det er et overraskende resultat, da det må anses for højst usandsynligt, at tungere hanner overlever dårligere end lette hanner. Men returraten hos hanner er ikke på samme enkle måde som hos hunner et mål for overlevelsen – mange hanner emigrerer og slår sig ned på andre ynglelokaliteter end UM. Og resultatet tyder stærkt på, at tunge hanner er mere tilbøjelige til at emigrere end lettere hanner. Dette bekræftes ved at se på ungevægten for hanner, der faktisk emigrerede (primært fugle genmeldt efter flere år og ikke set i UM); en relativt høj vægt af denne stikprøve var dog at forvente også af den simple grund, at den må rumme relativt færre hunner (fejlbestemt som hanner) end de mærkede unger som helhed, jf. Tabel 23.

Livstidsreproduktion hos hunnerne

En beregning af ungeproduktionen gennem hele levetiden, og ikke mindst variationen af denne livstidsreproduktion, må baseres på kohorter fra hvilke ingen fugle længere er i live. I databasen over UM gæssene er det derfor nødvendigt at se bort fra årgangene efter 1981, hvilket indebærer, at betydeligt mindre end halvdelen af materialet er anvendeligt i denne sammenhæng.

For hannerne er oplysningerne meget ukomplette, fordi en stor del ynglede andre steder end i UM. For hunnerne rummer databasen derimod næsten komplette oplysninger om ungeproduktionen. Et lille antal hunner slog sig dog ned og ynglede uden for UM, og for dem findes ingen eller kun ukomplette oplysninger. Det er heller ikke nøjagtigt kendt hvor mange gæslinger, hunnerne i databasen "repræsenterer", dvs. hvor mange hunlige gæslinger der i alt blev ringmærket i UM i de pågældende år. Et forsøg er på at estimere dette antal er gjort i Tabel 27, der også viser antallet af gæs fra disse årgange (1959-1981) i databasen, samt deres køn i den udstrækning det er kendt. Det faktiske antal hunner og hanner er forsøgt estimeret i Tabel 28. De 402 returnerede hunner svarer til 51% af de 794 mærkede, hvilket ser fornuftigt ud, og det usikre tal på 33 emigranter (4%) er også af en rimelig størrelse. Det kan måske umiddelbart forekomme usandsynligt, at (næsten) alle emigrerede hunner findes i databasen; men detaljerede undersøgelser i Skåne, med brug af halsringe der er lette at aflæse på stor afstand, har vist at emigrerende hunner slår sig ned inden for en afstand af 7 km fra fødestedet. Hvis det samme gælder UM gæssene, er der stor sandsynlighed for, at en emigreret hun på et eller andet tidspunkt vil blive aflæst i mosen.

Af de 369 hunner, der ikke emigrerede, forblev 279 længe nok i mosen til at de kunne kønsbestemmes med sikkerhed. De resterende ca 90 (24%) forsvandt, og er formentlig næsten alle døde før de nåede at yngle, om end ikke nødvendigvis alle sammen i deres andet leveår. Antallet af unger produceret af disse 279 hunner er vist i Tabel 29, idet kun minimumstal kan gives for i alt 17 "uregelmæssige" hunner – hunner der tilsyneladende eller med sikkerhed ynglede nogle år uden for UM. Disse ungetal svarer til nyligt klækkede unger; pga. adoption vides det ikke hvor mange af dem, der var i live ved slutningen af yngletiden, men i gennemsnit har ca 90% overlevet. Det betyder, at hvis de "uregelmæssige" UM hunner har reproduceret lige så godt som de regelmæssige, så bliver den samlede produktion på 1811 nyklækkede eller ca 1620 mærkningsmodne unger.

Af de 262 regelmæssige UM hunner nåede 241 en alder på i det mindste to år, og havde således mulighed for at yngle. Deres succes i den henseende er sammenfattet i Tabel 30, hvor den tilsvarende succes for hunner ringmærket som voksne er vist. De sidstnævnte gør det tydeligvis meget bedre end de unge-mærkede fugle, og forskellen er i virkeligheden endnu større end angivet – nogle af de adult-mærkede må nemlig have produceret en del unger før de blev ringmærket. Forskellen mellem unge- og adult-mærkede bunder primært i, at det tager flere år før en gås bliver fuldt kompetent som ynglefugl – bedømt ud fra de tidligere anførte resultater sker det ikke før en alder på omkring seks år, og mange fugle vil være døde før de bliver så gamle.

På den baggrund kan det ikke overraske, at der er en enorm variation i antallet af unger, som gæssene får (Tabel 30, Fig. 29). En anden måde at anskueliggøre det på er vist i Fig. 30. Næsten halvdelen af de 241 gæs (116) klækkede aldrig et kuld, mens det andet yderpunkt var en hun (#2473), der i løbet af sit 13 år lange liv klækkede 71 gæslinger. Ydermere udgør de 241 hunner kun ca 65% af dem, der overlevede det første år, og kun 30% af de gæslinger, der blev flyvefærdige; nogle af de sidstnævnte overlevede dog og slog sig ned og ynglede uden for UM.

Hvad afgør om en hun producerer mange unger? Et langt liv er i hvert fald en nødvendig betingelse, siden det mulige antal gæslinger pr sæson er begrænset til ca 10. Fig. 31 viser dog, at der også er en betydelig variation mellem hunner med samme livslængde. En tidlig ynglestart kunne være en anden betingelse, men skønt det – hvis yngleforsøget falder heldigt ud – vil sikre fuglen i det mindste noget afkom uanset hvor længe den siden overlever, så ser enhver fordel af en tidlig start ud til at være forsvundet efter det sjette eller syvende leveår (Fig. 32). Endelig kunne det have betydning hvornår hunnen er født. Ungeoverlevelse og førsteårsoverlevelse varierer mellem årene, og det gør fødebetingelserne under opvæksten givetvis også, noget der evt. kan mærke en fugl for livet. Ser vi alene på om hunnerne producerer eller ikke producerer unger, er der imidlertid ingen tegn på nogen mærkbar forskel mellem hunner fra forskellige år, bortset fra at hunner født i sidste halvdel af 1960erne havde meget ringe ynglesucces (Fig. 33).

Utterslev Mose som ynglehabitat for gæs

Sammenlignet med andre bestande af Grågæs ser gæssene i UM ud til at leve under meget gunstige betingelser. Bestandsstørrelsen er stor i forhold til arealet, dvs. bestandstætheden er ualmindelig stor, og ungernes overlevelse er endog meget høj. Desuden ser emigrationsraten ud til at være mindre end i andre bestande, noget som andre steder er fundet at have sammenhæng med fødebetingelserne på lokaliteten.

Betingelserne synes at have været fine helt frem til projektets afslutning i 1994, på trods af at bestanden var rundt regnet tre gange større end tidligt i perioden. I hvert fald er der ingen klare tegn på en tæthedsafhængig effekt i nogen af de betragtede parametre – hvor der overhovedet er en tendens over tid, kan den enklest forklares som en følge af et faldende jagttryk eller en mildning i klimaet gennem perioden. Dog kan den tilsyneladende svagt stigende emigrationsrate hos hannerne muligvis tydes som en tæthedsafhængig effekt.

Alligevel er det muligt, at bestanden var ved at nå et loft i 1994. Antallet af kuld, der har kunnet tælles i mosen, ser nemlig ikke ud til at være vokset siden sidst i firserne, om end det har varieret ganske betydeligt (Fig. 34). Det tyder på, at der kun er plads til, at et begrænset antal par kan yngle med held. Om det betyder, at et større antal par opgiver i rugetiden, eller om de helt undlader at yngle – fx således, at fuglene i gennemsnit bliver ældre, før de begynder at yngle – vides ikke.En lavere andel af ynglefugle i bestanden, og en lavere ynglesucces blandt ynglefuglene, var i projektets sidste år et naturligt resultat af, at gennemsnitsalderen i bestanden var lav som følge af den hurtige vækst. Men da totalbestanden jo næppe er fortsat med at vokse med samme fart, har andre forhold åbenbart påvirket ynglefrekvens og/eller -succes. Hvordan denne regulering mere præcist er sket, vides desværre ikke – projektet sluttede lidt for tidligt. Det er imidlertid vilkårene for sådanne langtidsprojekter – de starter gerne lidt tilfældigt og udvikler sig efterhånden, og de slutter ofte på en temmelig brat og uforudset måde.

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Photo: Knud Falk.

Appendix 1

Sexing Greylag goslings in Utterslev Mose, 1959-93

Most goslings were sexed when ringed 43 ± 8 SD days old (n=2398) during 1964 and 1966-93 (sexing was not attempted in 1959-63 and 1965). For birds that returned to Utterslev Mose (UM) in subsequent years it was possible definitively to determine the sex, permitting a 'quality check' of sex scores of goslings. The word 'returned' in the following hence means surviving for one or more years and settling in UM, or at least occurring there frequently enough and under circumstances so that the sex could be determined.

The difficulty is that the sample of returned birds is skewed sex-wise. But we may reasonably assume that the chance that a female returns do not depend on whether it was originally sexed as a female or a male, and similarly for males. More formally, using common symbols from probability theory we have that

$$\mathrm{P}(\mathrm{F} \cap \mathrm{M}_1 \cap \mathrm{R}) = \mathrm{P}(\mathrm{F} \cap \mathrm{M}_1)\ \mathrm{P}(\mathrm{R} \mid \mathrm{F})$$

$$\mathrm{P}(\mathrm{M} \cap \mathrm{F}_1 \cap \mathrm{R}) = \mathrm{P}(\mathrm{M} \cap \mathrm{F}_1)\ \mathrm{P}(\mathrm{R} \mid \mathrm{M})$$

where the indicated events are

F, M	a bird is a female (male), whether known or not to the observer
F_1, M_1	a bird is scored as a female (male) when ringed as a gosling
R	a bird returns and is sexed with certainty

In other words, we can estimate the probabilities of missexing

$$x = \mathrm{P}(\mathrm{M}_1 \mid \mathrm{F}) \quad \text{and} \quad y = \mathrm{P}(\mathrm{F}_1 \mid \mathrm{M})$$

by use of counts, viz. the numbers ff, fm (females originally scored as females and males, respectively), and mf, mm (same for males):

$$(1) \qquad x = \frac{fm}{ff + fm} \qquad\qquad y = \frac{mf}{mm + mf}$$

We may likewise estimate the true number of female (f_o) and male (m_o) goslings at ringing from the number scored as females and males (f_1, m_1):

$$(2) \qquad f_o = \frac{f_1 - (f_1 + m_1)y}{1 - (x + y)} \qquad m_o = \frac{m_1 - (f_1 + m_1)x}{1 - (x + y)}$$

and hence the return rates (probabilities)

$$(3) \quad r_F = \mathrm{P}(\mathrm{R} \mid \mathrm{F}) = \frac{ff + fm}{f_o} \qquad r_M = \mathrm{P}(\mathrm{R} \mid \mathrm{M}) = \frac{mf + mm}{m_0}$$

but again, note the special meaning of 'return' in this connection.

Finally, we may consider the probability that a bird was mis-sexed as a gosling

$$x_1 = \mathrm{P}(\mathrm{F} \mid \mathrm{M}_1) \quad \text{and} \quad y_1 = \mathrm{P}(\mathrm{M} \mid \mathrm{F}_1)$$

As stated initially, however, these probabilities differ between the population and the returned sample:

$$(4) \quad \text{Population} \qquad x_1^{\,p} = \frac{f_o x}{m_1} \qquad y_1^{\,p} = \frac{m_0 y}{f_1}$$

$$(5) \quad \text{Returned sample} \quad x_1^{\,r} = \frac{fm}{fm + mm} \qquad y_1^{\,r} = \frac{mf}{ff + mf}$$

Inevitably, x_1^r will be inflated and y_1^r reduced relative to x_1^p and y_1^p, owing to the fact that almost all surviving females but only a proportion of the males return, so mis-sexed 'males' (i.e., females) are much more likely to return than correctly sexed 'males', while the opposite is true for 'females'.

The considerations so far assume that all goslings were sexed at ringing. This is not the case, however, and this fact complicates the discussion. However, 319 (72%) of the 442 unsexed goslings were born in the six years where sexing was not even attempted, and also the remaining 123 (with the exception of 30 and 31 tentatively assigned as being females and males, respectively) were left unsexed because of time constraints or other causes not possibly connected with the true sex of the goslings. Accordingly, the sex ratio of the unsexed subsample should not deviate from that of the full sample.

Corrected numbers f_o' and m_o' of ringed females and males, hence, are simply f_o and m_o upscaled by the factor (total goslings)/(sexed goslings). The return rates (3) might then be replaced by

$$(3^*) \qquad r_F = \frac{f\cdot}{f_o'} \qquad\qquad r_M = \frac{m\cdot}{m_o'}$$

where $f\cdot$ is $\Sigma_x fx$ (the total number of female geese sexed after returning one or more years after ringing), and similarly for $m\cdot$.

Appendix 2

Maximum likelihood estimation using MARK

It would be preferable to estimate survival for the various population segments of the Greylag Geese in Utterslev Mose in a more systematic way than presented in the main text, although the application of a systematic technique to estimate a parameter does not *per se* render the result superior to estimates obtained by other methods.

The main deficiency of the method used to estimate survival in the text was that it did not distinguish between the effects of mortality and emigration. This was particularly unfortunate in the case of the young birds, although it might well be that the emigration rate in females was sufficiently small as to be negligible. Modern techniques are potentially able to overcome such difficulties.

Program MARK (Cooch & White 2002) is a versatile tool for analysing data from marked animals, offering techniques for a variety of data types and great flexibility in choice of models. At present, MARK is the most comprehensive program in existence for such analyses, incorporating parts from several other software applications of more specific utility.

Generally, for each specified model, MARK estimates the parameters and their standard errors and confidence intervals, and in addition calculates the model's deviance (lack of fit of the data to the model) and some parameters indicating the merits of the model relatively to other models considered for the same data. Models will fit the data better the more parameters they contain (provided the model structure is reasonably 'sound'), but models with fewer parameters will provide better parameter estimates (narrower confidence intervals). The AIC (Akaike's Information Criterion) is a function that decreases with increasing model likelihood and increases with number of parameters and thus compromises between these conflicting considerations – usually, if a new model can be constructed with fewer parameters without an unduly reduced fit to the data, it is to be preferred. For each of the considered models, MARK gives the absolute value of AIC, the difference between AIC and the AIC of the currently 'best' model (ΔAIC), an AIC weight calculated on basis of ΔAIC, and a relative model likelihood that is actually a renormalized AIC weight with a value of 1 for the 'best' model.

Combined re-sighting/recovery analysis

MARK offers the possibility of analysing combined re-sighting and recovery data following Burnham (1993). In such an analysis, four types of parameters are estimated: S, the year to year survival probability; p, the re-sighting probability (given that the bird is alive and has not emigrated); r, the probability that a dead bird is reported; and F, the fidelity parameter, i.e., the probability that a surviving bird has not emigrated. However, when considering such an analysis on the UM goose data, several problems become immediately apparent.

1) The model describes the dynamics of the actual population rather coarsely. Parameters may vary between age groups and sexes, but in the real population they must also vary in a complex way depending on, e.g., attachment to UM that year, breeding status, etc. Besides, the model considers permanent emigration but not temporary emigration or the skipping of single years, the occurrence of which may obscure the distinction between the p and F parameters, and very likely influence the estimates of the other parameters as well. At the very least, the interpretation of the re-sighting parameter must be changed from the intended meaning, the probability that a present bird will be seen, to the probability that a bird is present and will be seen – in reality, the probability that it will be seen *if* present is probably very close to unity in the UM dataset. The lack fit between the model structure and the data could be grave enough as to render the results meaningless, or it could be slight and in practice insignificant. It might be quantified by use of simulating techniques, but for a dataset like the present this would take a computer with considerably more power than most PCs.

2) Of the other problems, the most serious is probably the uncertain sex determination of goslings. There is ample evidence that sex do matter for the probability of returning to and settling at UM, and it could also have a significant influence on survival and the risk of being shot (hence the chance of being recovered). The occurrence of erroneously sexed goslings implies a blurring of any sexual differences in the estimates of these parameters. This should especially influence the estimates for the younger age classes, since most geese staying at UM and surviving for more than a few years were sexed with certainty. Unfortunately, most emigrating birds are young, so emigration rate estimates could be seriously flawed.

3) In recovery analyses, the combination of birds ringed as young and birds ringed as adults is necessary in order to obtain meaningful estimates of age-specific survival (Brownie et al. 1985). In a combined analysis as here discussed it will be advisable likewise to include both 'young' and 'adults' (although a young-only dataset given as an example in Cooch & White (2002) gave reasonable results). The assumption inherent in such cases is that birds ringed as chicks survive and behave like birds ringed as adults when they are old enough. However, there were some indications that this may not be strictly true in the UM dataset. Furthermore, the rather small size of the adult-ringed sample could be a problem.

Combined analyses of the UM dataset were run using MARK, but considering the mentioned uncertainties concerning the reliability – and the interpretation – of the results, these are only briefly summarized here. The size of the dataset made it impractical to run a single analysis

Table A1. Estimates of parameters from combined analyses of recapture (re-sighting) and recovery data. From the preferred models, combining geese ringed as adults and young, for females and males separately. Estimates are shown as mean ± SE, except for first-year survival, where the preferred models involved time-dependence; here the table shows unweighted mean ± SD of the annual estimates.
Estimerede parametre opnået ved kombineret analyse af observationer og genfund af ringmærkede UM gæs (ML estimater fundet vha. programpakken MARK). Modellen opererer med fire parametre, der alle i princippet kan afhænge af alder og år: 1) sandsynligheden for at overleve til det følgende år ('survival parameter'), 2) sandsynligheden for at blive set og registreret i løbet af året, forudsat at fuglen ikke er emigreret ('recapture parameter'), 3) sandsynligheden for at en fugls død bliver kendt, dvs. at ringen findes og rapporteres ('reporting parameter'), og 4) sandsynligheden for at en fugl undlader at emigrere ('fidelity parameter'). Tre overlappende delperioder er betragtet, og i de "bedste" modeller inden for hver var alle parametre tidsuafhængige, med undtagelse af overlevelsen i første leveår (her viser tabellen gennemsnit og standardafvigelse af de årlige værdier). Hvor intet estimat er anført, angav modellen samme værdi som for de adulte.

Det er klart, at Grågæssene i Utterslev Mose ikke helt opfører sig i overensstemmelse med modellen. Bl.a. kan de, især i de unge år, helt udeblive fra mosen (modellen tillader kun permanent emigration). Desuden er usikkerheden i kønsbestemmelsen af gæslingerne et problem, fordi hunner og hanner opfører sig forskelligt (især mht. emigration), og fordi kønnet kun kunne kontrolleres og evt. rettes for de fugle, der overlevede og slog sig ned i mosen.

	First year		Second year		Adults	
	females	males	females	males	females	males
	Survival parameter S					
1966-78	0.530 ± 0.158	0.487 ± 0.176	–	–	0.768 ± 0.020	0.782 ± 0.022
1974-86	0.550 ± 0.226	0.476 ± 0.155	0.764 ± 0.031	0.640 ± 0.045	0.811 ± 0.021	0.746 ± 0.022
1982-94	0.654 ± 0.135	0.511 ± 0.151	0.750 ± 0.023	–	0.803 ± 0.014	0.808 ± 0.020
	Recapture parameter p					
1966-78	0.863 ± 0.028	0.775 ± 0.046	0.956 ± 0.021	0.797 ± 0.051	0.907 ± 0.019	0.874 ± 0.021
1974-86	0.825 ± 0.026	0.713 ± 0.048	–	–	0.964 ± 0.009	0.911 ± 0.016
1982-94	0.816 ± 0.019	0.681 ± 0.035	0.958 ± 0.012	–	0.986 ± 0.005	0.900 ± 0.013
	Reporting parameter r					
1966-78	–	–	–	–	0.431 ± 0.028	0.404 ± 0.027
1974-86	–	–	–	–	0.326 ± 0.022	0.366 ± 0.021
1982-94	–	0.229 ± 0.025	–	–	0.257 ± 0.017	0.332 ± 0.033
	Fidelity parameter F					
1966-78	0.917 ± 0.034	0.756 ± 0.057	–	0.814 ± 0.061	0.963 ± 0.018	0.955 ± 0.024
1974-86	–	0.661 ± 0.054	–	0.825 ± 0.067	0.937 ± 0.017	0.969 ± 0.018
1982-94	–	0.722 ± 0.057	–	0.777 ± 0.045	0.973 ± 0.010	0.939 ± 0.022

of four groups (females/males ringed as goslings/adults) over the entire study period. Instead, two combinations ('young' and 'adult' females, 'young' and 'adult' males) were each considered in three overlapping 13-year periods between 1966 and 1994.

Results

The estimated parameters of the preferred models are shown in Table A1. For the time-dependent first-year survival, the means over the subperiods are shown; the annual values correlated well with the survival probabilities estimated from returns (Fig. 10) (females: $r = 0.983$, $P < 10^{-18}$; males: $r = 0.947$, $P < 10^{-13}$). For the period covered by Fig. 10 – 1966/67-1993/94 – the mean was 0.571 ± 0.180 SD for females, 0.483 ± 0.147 SD for males. For females this is similar to the unweighted mean of the return rates in Fig. 10 (0.540 ± 0.185 SD, $t = 0.625$, $P = 0.53$), whereas in males the mean return rate is much lower (0.374 ± 0.112 SD, $t = 3.131$, $P = 0.003$). Since emigration is a confounding factor in the survival estimates based on returns, but not in the maximum likelihood estimates, these results appear to confirm that very few females emigrate, whereas many males do. However, a tendency towards lower survival of young males than of young females is still apparent in the MARK results, and although this may be a real difference it could well be artificial, an effect of emigration caused by a mismatch between model and reality.

For no other parameter was any time-dependence suggested within the period in question, neither in the preferred model or in other reasonably 'likely' models, but some differences between periods were indicated.

Survival S: Apart from a time-independent 'adult' survival and the time-dependent first-year survival, a separate (constant), intermediate second-year survival was indicated for some periods. There was some indication of an improving adult survival from the first period to the last.

Re-sighting p: There was no time-dependence, but some indication of an increase from one period to the next in adult females. Irrespective of age, values were higher for females than for males. First-years had lower values than older birds. A separate second-year p-value was suggested for some periods. Some of these findings are unexpected and suggestive of age- and sex-dependent probabilities of frequenting UM rather than differences in the chance of detecting present birds.

Reporting parameter r: Little evidence of time- or age-dependence, but a clear decreasing trend from the first to the last period. This is a reflection of the decreasing recoveries of shot birds also mentioned in the main text.

Fidelity parameter F: Little evidence of time-dependence within or over periods, or of age-dependence in females, whereas first- and second-year males had lower values than adults. For adult males the fidelity to UM seemed to be just as high as for females. Despite the high F for adults, MARK is likely to underestimate it, assuming that birds skipping the last year(s) before being recovered have emigrated.

Recovery analysis

As a supplement to the re-sighting/recovery analyses, a traditional analysis of recoveries according to Brownie et al. (1985) (shot birds only) was attempted, with the main purpose of estimating the recovery rate f, the probability that a bird alive at the beginning of a given year is shot and reported during that year (f is connected with the formerly defined survival (S) and reporting (r) parameters by the relationship $f = (1-S)\cdot r$). Since the recovery matrix was rather thin, sexes were combined in a single matrix. This also permitted the inclusion of the early years where goslings were not sexed. The periods considered were 1959-1974, 1969-1984, and 1979-1994, having sufficiently large overlapping periods that only 18 recoveries out of 1003 had to be sacrificed in making the subdivision.

The analysis indicated time-independent survival rates for adults as well as first-year birds – for adults 0.753 ± 0.025 SE, 0.723 ± 0.028 SE, 0.769 ± 0.028 SE, for the three periods considered, and for first-year birds 0.651 ± 0.113 SE, 0.659 ± 0.095 SE, 0.494 ± 0.092 SE. These estimates must surely be inferior to the estimates reported in the main text. For adults even the recovery parameter came out as time-invariant: 0.082 ± 0.013 SE, 0.067 ± 0.011 SE, and 0.063 ± 0.009 SE for the three periods considered, suggesting a decrease during the study period. The analysis only considers shot birds that were retrieved and reported and will underestimate the actual hunting pressure. For first-year birds the recovery rate was time-dependent and very similar to the proportion of ringed goslings that were shot during the following year (cf. Fig. 14).