Change of mate in a Greylag Goose *Anser anser* population: effects of timing on reproductive success

L. Nilsson & H. Persson

Department of Animal Ecology, University of Lund, Ecology Building, S-223 62 Lund, Sweden.
Email: leif.nilsson@zooekol.lu.se.

The population of the West Baltic Greylag Goose Anser anser *is migratory, breeding in southwest Scania, southernmost Sweden and wintering in the Guadalquivir Marismas, southwest Spain, or in the Dutch Delta. This population has been the subject of a long-term study of a sample of neck collared individuals, and observations of marked individuals were used to assess rates of mate fidelity in this supposedly long-term monogamous species. The annual divorce rate during the years 1985-2000 was 10.5% (n=415), with 29.7% of all pairs ending in a divorce (n=158). After divorce or death of the partner, birds re-paired assortatively with individuals from their own breeding area, using the same wintering area. New pair bonds formed on the breeding area, during one of three periods; just after return in spring, just after moult and just before departure in autumn. Divorce or partner death during the period 15 October - 28 February, when breeders were away from the breeding grounds, resulted in a significantly lower reproductive success during the following breeding season, compared to mate losses during the period 1 June - 14 October.*

Key Words: Mate-change, divorce, pair-formation, breeding result, Sweden

True geese (genera *Anser* and *Branta*) are generally considered to be long-term monogamous. Our knowledge about mate fidelity and its evolutionary significance in northern nesting geese is, however, meagre. Mate change may come about as a result of either the death of partner or divorce, where divorce is defined as a "pair break-up at any time of the year

when both partners are still alive and where the subsequent breeding attempt, if any, of at least one bird is with another partner" (Choudhury 1995). Among most studied species exhibiting long-term pair bonds, a change of mate results in a temporary reduction in reproductive performance (Coulson 1972; Ollason & Dunnet 1988; Bradley *et al.* 1990; Black *et al.* 1996; Rees *et al.* 1996). The temporary nature of this reduction suggests that some time factor is involved in the development of a new pair bond. If this is so, and the time required to compensate for the costs associated with change of mate is shorter than one year, it would be predicted that the point in the annual cycle at which divorce or partner death occurs will affect breeding success in the following year.

To test for the effects on reproductive success of the timing of divorce and partner death, data were used from a long-term study of neck collared West Baltic Greylag Geese *Anser anser*, breeding in southwest Scania, southernmost Sweden (Nilsson 1998). This population is fully migratory, using two main wintering areas. When the study started in 1985 about 90% of the breeders wintered in the Guadalquivir Marismas, southwest Spain. Throughout the study period the Dutch Delta gained in importance, and today less than 20% of the breeders are found in Spain in winter. Departure from the breeding area in autumn and return in spring varies markedly among years and individuals, but during the study period, breeders were present on the breeding area, on average from the beginning of March until the middle of October (Nilsson & Persson 1992, 1994, 1998 and unpublished data).

Methods

Greylag Goose families have been captured and neck collared annually in a study area in southwestern Scania, southernmost Sweden since 1985 (Nilsson & Persson 1992; Persson 1994). A total of 575 adults and 1,700 goslings were neck collared up to 2000 (Persson 2000).

Between 1985-2000, regular searches for neck collared geese were undertaken from their spring arrival until their autumn departure. In spring, the study area was visited several times a week in order to establish the return of marked birds and their breeding performance. From late May until the last young were fledged, the breeding area was visited almost daily to establish the number of fledglings in each family. In summer and autumn, weekly searches were extended to include neighbouring staging areas, especially the Foteviken area at the coast, where a large proportion of the Greylag Geese from the study area gather at this time of year (*cf.* Nilsson & Persson 1992).

Re-sightings from other parts of the flyway were obtained from a network of volunteers. These data were supplemented by intensive field work by HP on the staging and wintering areas, mainly in the Guadalquivir Marismas and at Villafáfila, but occasionally also in other

areas in Spain, as well as in all major haunts in the Netherlands, Belgium and France.

Due to a very high re-sighting frequency all year round (Nilsson & Persson 1993) it was possible to establish in all but a few cases during which part of the annual cycle a death of partner or divorce had taken place. In most cases, this interval could be narrowed down to less than a month, sometimes to a specific day. Exact timing of divorce and death of partner was often impossible to establish during nesting, as the nest sites were rarely visited. The same applied to fail-breeders during their annual wing moult, as it usually took place in inaccessible places (Nilsson *et al.* 2001). The re-sighting frequency was lower when the geese were away from the breeding grounds compared to when present (Andersson *et al.* 2001). In some cases, there were no re-sightings available from the period the pairs were away from Scania.

Determination of pair bonds was facilitated by all individuals being neck collared. Two adult individuals of opposite sex were considered as a pair if they were closely associated, when not being alone. Greylag Goose mates stay close to each other all year round, but the distance increases during incubation, when males sometimes feed alone.

Divorce rate was calculated as the number of divorce events divided by total number of pair-years, where a pair-year was when both pair members in year *t* survived to year *t*+1.

Reproductive success was defined as the percentage of breeding attempts (real and potential) that resulted in at least one fledgling (*cf.* Nilsson & Persson 1996). When a former breeder was unmated during a breeding season it was counted as a potential breeding attempt. In cases when death of a partner was preceded by a divorce in the same year, the surviving mate was counted as divorced.

The annual cycle was divided into two main parts depending on whether the breeders were present or absent from the breeding grounds, with 1 March and 15 October as approximate dividing dates. The period when birds were present on the breeding grounds was further divided into: breeding until wing moult, wing moult, post-fledging and autumn. The wing-moult period lasted about one month and commenced during the last days of May or the first two weeks of June among breeders, somewhat earlier among fail-breeders. The post-fledging period, when families stayed close to their brood-rearing areas, lasted until the end of July. Even though the exact timing of the different parts of the annual cycle varied among years, fixed time periods were used in the main analyses.

Results

Death of partner

The average annual mortality among breeders in the study population was estimated to be 16.1%±1.4 (Nilsson & Persson 1996). Marked variation among geese using different wintering areas and among years were related to differences in hunting pressure (Nilsson & Persson 1996; Persson 1996, 1999); the annual mortality was almost three times as high among birds wintering in southwest Spain compared to those wintering in the southwest Netherlands. (22.0%±1.5 and 7.8%±1.9 respectively). Overall, 81.7%±3.5 of all deaths of partners occurred during the open season for this species (**Table 1**). Most other deaths occurred during the nesting period, mainly females killed by predators or dying of other causes while incubating.

Divorce

The divorce rate during the years 1985-2000 was 10.5%±1.5 (n=419 pair-years), with 29.7%±3.6 of all pairs (n=158) ending in a divorce. Divorce rate was markedly higher among pairs wintering in the Guadalquivir Marismas compared to those wintering in the Netherlands, 12.2%±2.4 (n=188 pair-years) vs 7.6%±1.9 (n=185 pair-years), but the difference was not significant (χ^2=2.27, n.s.). For most divorced birds it is not known whether they chose to divorce or were the victim. The distribution of divorces over the annual cycle largely resembles that of deaths of partners (**Table 1**).

Table 1. Number of deaths of partners and divorces recorded during different parts of the annual cycle, in a breeding Greylag Goose population in Scania, 1985-2000.

Part of annual cycle	Death of Partner	Divorce
Breeding until wing moult	15	13
Wing moult	3	3
Post-fledging	3	3
Autumn	24	14
Migration + wintering	74	32
Total	120	65

Timing of pair formation

The formation of new pair bonds following the death of a partner or divorce was recorded in 86 cases. All pairs formed in the breeding area, during one of three periods: 6 February - 20 March (n=37), 26 June - 21 July (n=34) and 28 August - 14 October (n=15). We have no indication that new pairs were formed during other times of the year.

Reproductive success

In pairs with unbroken pair bonds, the reproductive success (the percentage of breeding attempts resulting in at least one fledged young) was, on average, significantly higher in year t than in year t+1 (64% vs 53%, n=418 pair-years, (χ^2=9.98, P<0.01). One reason for this is that catching for neck collaring takes place when goslings are about six weeks old (Persson 1994). As a consequence, a large proportion of the adults enter the study population as successful breeders.

The reproductive success was significantly lower in the season after change of partner compared to the preceding season, both following the death of partner (**Table 2**) and divorce (**Table 3**). The reduction in success was most marked for deaths and divorces occurring during the period when most geese were away from the breeding grounds. There was a slight reduction in reproductive success also after deaths and divorces occurring during the rest of the year, but these were not significant. A male losing its mate during nesting cannot obtain a worse reproductive success during the following breeding season and the same might be true for females. Only fail-breeders divorced during the early part of the breeding season (**Table 3**).

Birds losing their partner during the period 1 June - 14 October had a signif-

Table 2. Reproductive success (percentage of breeding attempts resulting in at least one fledgling) in the season immediately preceding and succeeding death of partner, in relation to when the death occurred.

Time of year	n	Before	After	χ^2	P
1 March - 31 May	15	20%	20%	0.00	n.s.
1 June - 14 October	31	61%	52%	0.59	n.s.
15 October - 28 February	74	72%	31%	24.34	<0.001
1 June - 28 February	110	67%	37%	19.84	<0.001

Table 3. Reproductive success (percentage of breeding attempts resulting in at least one fledgling) in the season immediately preceding and succeeding a divorce, in relation to when the divorce took place.

Time of year	n	Before	After	χ^2	P
1 March - 31 May	11	0%	36%	4.89	<0.05
1 June - 14 October	39	46%	36%	0.85	n.s.
15 October - 28 February	49	61%	16%	20.80	<0.001
1 June - 28 February	88	55%	25%	16.03	<0.001

icantly higher reproductive success during the following breeding season compared to those losing their partner during the period 15 October - 28 February, independent if it was due to death (**Table 2**, χ^2=3.94, P<0.05) or divorce (**Table 3**, χ^2=4.43, P<0.05).

Discussion

The divorce rate found in this study is similar to that reported for a sedentary Greylag Goose population in Austria, but markedly higher than rates found in most other goose species (summarised by Black *et al*. 1996), as well as in swans (Rees *et al*. 1996). The divorce rate was significantly lower during the first ten years of the study (Leif Nilsson in Black *et al*. 1996) compared to the following five years (5.1%, n=292 vs 22.8%, n=127, (χ^2=29.49, P<0.001), during which period the number of breeding pairs increased from 120 in 1985 to 525 in 1995 and 720 in 2000 (Nilsson & Persson unpublished

data). Mean reproductive success has declined as the population has increased (Nilsson & Persson unpublished data), which ought to have facilitated increased frequency of divorce, by lowering the long-term costs associated with divorce.

Divorce was more frequent during periods and amongst those sub-populations experiencing higher mortality rates. The reason might be that higher frequency of death of partner makes for a larger pool of unattached birds, potentially of better quality than an existing partner. In the Barnacle Goose *Branta leucopsis*, divorce increased with the number of experienced breeders becoming available due to death of partner (Black *et al*. 1996). Such a relationship is in accordance with the *better option hypothesis*, in which divorce occurs when one member of a pair is able to improve its reproductive success by obtaining a better quality mate (Ens *et al*. 1993). However, this was not

the sole reason for divorce in our study area, as we observed *forced divorce* (Choudhury 1995) as well as (temporary) divorce after *accidental loss* (Owen *et al.* 1988). In two cases, an old male displaced a male of unknown age and took over its mate, as well as the brood of newly-fledged young. In both cases, the usurper had lost its former mate during nesting about three months earlier, and displaced the sitting male as soon as the usurper had returned to his former breeding lake, having moulted elsewhere. In another case, a male injured by a lead pellet while wintering in Spain, returned to the breeding lake about a month after the former partner had started to breed with a new mate. But, when the female came with young ten days later, the former pair bond was re-established.

Reproductive success of individuals was, as found in most studies, lower in the year after divorce or partner death than the year before. However, caution is needed when interpreting these values, as the results are inflated by most birds being neck collared as successful breeders. In pairs where at least one of the mates had breeding experience, excluding the first breeding of a bird neck collared as gosling, as well as the year of neck collaring for those marked as breeders, 48.5% (n=1,335) of all breeding attempts resulted in at least one fledgling during the years 1986-2000. Substituting the values for "Before" in **Tables 2 and 3** with a value of 48.5% does not change the outcome of the statistical tests for the periods 1

June - 14 October and 15 October - 28 February, even if the significance level is lowered in one case (to $P<0.05$ for death of partner 15 October - 28 February). Thus, there are good reasons to accept the obtained results as representative of the true effects of partner change on reproductive success.

At the moment there is no explanation to the low reproductive success of birds whose former mate had died during the preceding breeding season. It might be that mateloss during this part of the annual cycle markedly affects the likelihood of the survivor to establish a relationship leading to successful breeding.

There is strong evidence that birds from the study population re-pair assortatively with individuals from their own breeding area, using the same wintering area. First, all breeding dispersal in this population occurred within the study area, in no case exceeding 6 km. Only 1.5% of the males and 0.5% of the females changed breeding site between successive years. Secondly, breeders were found in the same wintering area (Guadalquivir Marismas, Villafáfila or Dutch Delta) as in the preceding winter in as much as 99.2% of the cases (Nilsson & Persson 1996). Moreover, there is a strikingly close match of mortality rate and divorce rate for birds wintering in the Dutch Delta (7.8% vs 7.6%), less so for those wintering in the Guadalquivir Marismas (22.0% vs 12.2%). However, if survival rates were corrected for cases

when both mates were shot at the same time (extremely rare among birds wintering in the Netherlands but fairly common among those migrating to southwest Spain, *cf.* Persson 1996), a corresponding match would most likely be found for birds wintering in the Guadalquivir Marismas.

New pair bonds formed, in contrast to what is generally believed to be the rule in geese, on the breeding area during one of three periods: just after return in spring, just after moult and just before departure in autumn. It cannot fully be ruled out that new pair bonds were also formed during the prenuptial migration, as some new pair bonds were established when observed for the first time after arrival on the breeding area. However, taking into account that the breeding area was not checked daily and how fast pair bonds can form in spring, it also seems likely that these pair bonds were established on the breeding area. This is even more likely when it is considered that new pair bonds have never been recorded on prenuptial stop-over sites, not even at Foteviken Bay, situated only 20 km from the breeding area.

The existence of three annual periods during which re-pairing takes place gives a bird much more time to find a new mate when losing its former partner in spring, summer or early autumn compared to in late autumn or winter. Most individuals formed new pair bonds during the first re-pairing period occurring after partner loss, sometimes within days of a divorce, while

some birds remained unpaired from one spring to the beginning of next breeding season. Less than 20% remained unpaired four months after divorce/loss of partner, and hardly any after eleven months. The time to replace a lost mate varies considerably within species, as well as among closely related species. It is reported to take between three and nine months in the Barnacle Goose (Black *et al.* 1996). Mute Swans *Cygnus olor* are thought to re-pair within weeks following loss of mate, while the mean time to re-pair was 2.6 years in Bewick's Swans *Cygnus columbianus bewickii* and 1.9 years in Whooper Swans *Cygnus cygnus* (Rees *et al.* 1996).

While a divorce or partner death after mid-October resulted in a marked reduction in reproductive success, that was not the case if it occurred before mid-October. Thus, a period of five months seems to be sufficient for pair partners to establish a relationship for successful breeding, while the time available after return to the breeding area in spring in most cases was evidently too short to facilitate a successful breeding attempt.

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