Possible density-dependence in an expanding population of Greylag Goose *Anser anser* in south Sweden

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Abstract

Neck-banded Greylag Geese *Anser anser* breeding in southwest Sweden were studied from 1984–2012 inclusive, to determine annual variation in the number of breeding pairs, reproductive success and survival rates, as part of a larger programme of monitoring individual geese across the Nordic countries. Numbers breeding in the study area increased from 120 pairs in 1984 to 1,240 pairs in 2008, followed by a decrease to about 800 pairs. As the number of nesting pairs of Greylag Geese increased, the proportion of pairs producing young decreased, suggesting density-dependence effects on the production of young. The decline in the proportion of breeding pairs occurred later at a lake thought to offer better feeding areas for the young than at a second lake in the study area. There was no marked decrease in the mean brood size among productive pairs, only a slight decrease in the fledging rate. There was also no clear trend during the study in first-year survival rates for geese neck-banded at fledging.

Key words: breeding numbers, density-dependence, fledging success, Greylag Goose, south Sweden.

Fifty years ago, the Greylag Goose was a rare breeding species in the Nordic countries, with an estimated 300 pairs nesting in Sweden (Ottosson *et al.* 2012). During the 1970s, however, numbers started to increase markedly not only in Sweden but also across the rest of Europe (Nilsson *et al.* 1999). Annual early autumn surveys of Greylag Geese were initiated in the Nordic countries in 1984 to monitor the changes in numbers (Nilsson 2013), and these counts continue under both the national monitoring programmes and the mid-winter International Goose Counts coordinated by Wetlands International. Since the counts commenced in 1984, the number of geese recorded in Sweden during the September counts has increased from *c.* 20,000 birds during the early 1980s to 250,000 individuals by 2009 (Nilsson 2013), with an estimated breeding population of *c.* 41,000 pairs (Ottosson *et al.* 2012). Over the same period, the Greylag Goose breeding distribution has expanded across large parts of the country, with the exception of the taiga zone.

Better to understand the changes in migration patterns and in breeding numbers of Greylag Geese in the Nordic countries, a Greylag Goose neck-banding programme was started in 1984 (Anderson *et al.* 2001). Since 1985, monitoring of the species in Sweden has also involved detailed studies of the marked individuals, to determine numbers of breeding pairs, their productivity, survival rates and recruitment to the breeding population at five lakes in the southernmost part of the country (Nilsson 1998; Nilsson *et al.* 1997, 2002; Nilsson & Kampe-Persson 2003; Nilsson & Persson 1994, 1996, 2001a, b).

Over the last ten years, there appears to have been a decrease in productivity amongst geese breeding at some of the lakes. At the same time, total numbers counted in September ceased to increase (Nilsson 2013) and started to decline (Nilsson & Haas 2015). Detailed data from the study in southernmost Sweden therefore were analysed, and the results presented here, to determine which factors might be affecting Greylag Goose productivity in the region.

Study area

The study was undertaken at five breeding lakes in southern Sweden (Fig. 1) but at two of the lakes (Klosterviken and Yddingen) we attempted to determine whether breeding density influenced goose productivity, because they provided good opportunities to keep track of all breeding pairs and their offspring after hatching. At the other three lakes in the study area, it was difficult to find all broods, although data on neck-banded Greylags from all lakes were included in the analyses. The five lakes are situated in a rolling landscape with agricultural areas mixed with patches of mostly deciduous (beech) forest. They are all typically eutrophic and have extensive reed beds along parts of the shoreline. There are also some islands in two of the lakes, and all five lakes are surrounded by meadows where the adults and young can graze.

Lake Klosterviken is a small lake (16 ha) surrounded by reed beds and well-grazed meadows. Lake Yddingen is larger (190 ha) and situated in a more open landscape, with extensive reed beds along some sections of the shoreline, plus a few islands in the lake that provide breeding habitat for the geese. Yddingen borders a golf course, which offers excellent feeding conditions with short nutritious grass at the site over the entire breeding season. A few ponds with small islands on the golf course are also good breeding areas for the geese and, in addition to the golf course, there are meadows adjacent to the lake which are grazed by the geese at Yddingen.

Nilsson & Persson (1994) and other papers cited in the introduction give more details about the study sites, especially Nilsson *et al.* (2002) which includes maps of the feeding areas used by the broods.

Methods

A total of 2,639 Greylag Geese (664 adults; 1,947 young) was neck-banded in the study area in southwest Sweden during 1984–2008. These yielded, a total of 100,500

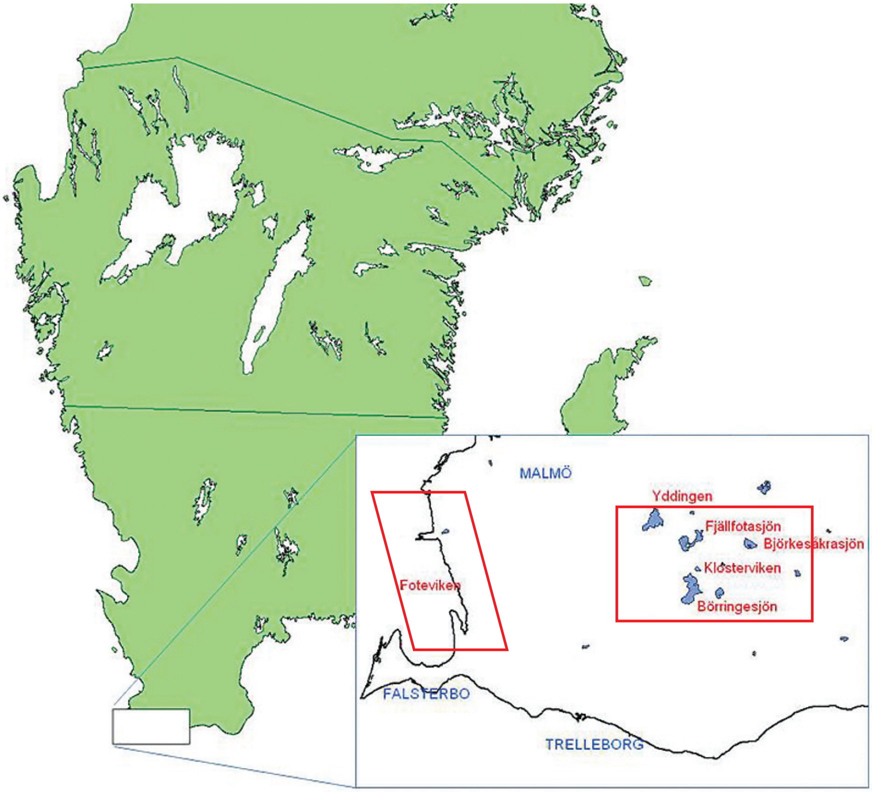

Figure 1. Map of south Sweden showing the Greylag Goose study area in an inserted map. Foteviken at the coast is the main autumn staging area, where a large proportion of the neck-band readings were made.

local observations and 15,200 sightings of individual birds made outside the marking areas, which were included in the analyses. The catching and marking programme is described in detail in Andersson *et al.* (2001).

From 1985 onwards, all potential Greylag Goose feeding areas were searched intensively for geese several times a week during early spring, to count the number of pairs present before they dispersed for nest-building (Nilsson & Persson 1994). The pair status of both marked and unmarked geese was established by observations made of their behaviour. During the entire spring and early summer the area was also checked for neck-banded Greylag Geese at least twice a week (often simultaneous with the counts made of paired birds) to establish their survival, arrival patterns, pair-bonds and the production of young. Once the goslings had hatched, intensive surveys of all feeding areas around the lakes were undertaken several times a week. Families with neck-banded adults were checked for fledglings over the summer, and the number of fledged young associated with all marked adults was established annually. In the analysis presented here, fledging success was calculated as the total number of fledged young each year, measured as a percentage in relation to the total number of newly-hatched young recorded, for all marked families at the two lakes. Fledging success was estimated only for years in which data were available both on the number of newly-hatched young and on the number of fledged young at each site. Intensive surveys for neck-banded Greylag Geese were also organised on staging and moulting areas in Sweden and through the entire European flyway and wintering areas, yielding an extensive database with breeding records of individual geese with known breeding status, migration patterns, and staging and wintering habitats.

Linear regression analysis was used to determine trends over time in the numbers of breeding pairs at the two main lakes (Lake Klosterviken and Lake Yddingen), and to assess relationships between the pair counts and productivity measures recorded for Greylag Geese during the study.

Results

A pair of Greylag Geese seen with young was the first evidence of breeding in the study area in the late 1960s. When regular counting of geese in the study area commenced in 1985, 120 pairs were present, which increased to peak at 1,240 pairs in 2008 after which numbers fell to *c.* 800 in 2012 and 2013 (Fig. 2).

At Lake Yddingen, the number of breeding pairs increased from 26 in 1985 to a peak at *c.* 600 in 2008, but then declined (Fig. 3). At the smaller Lake Klosterviken, 25 pairs were found to be breeding in 1985,

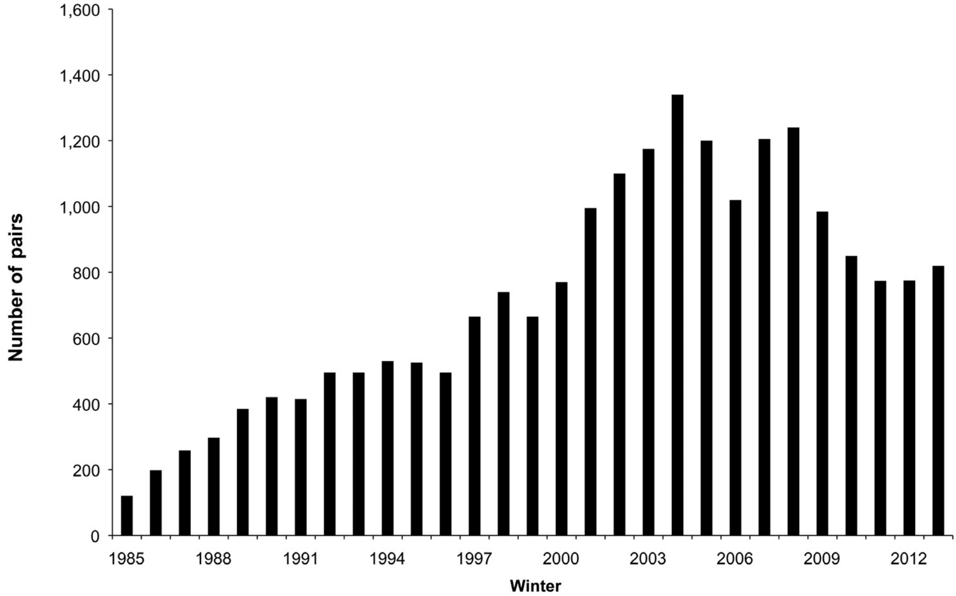

Figure 2. Number of breeding pairs of Greylag Geese recorded in the study area in southwest Sweden during early spring surveys, 1985–2013.

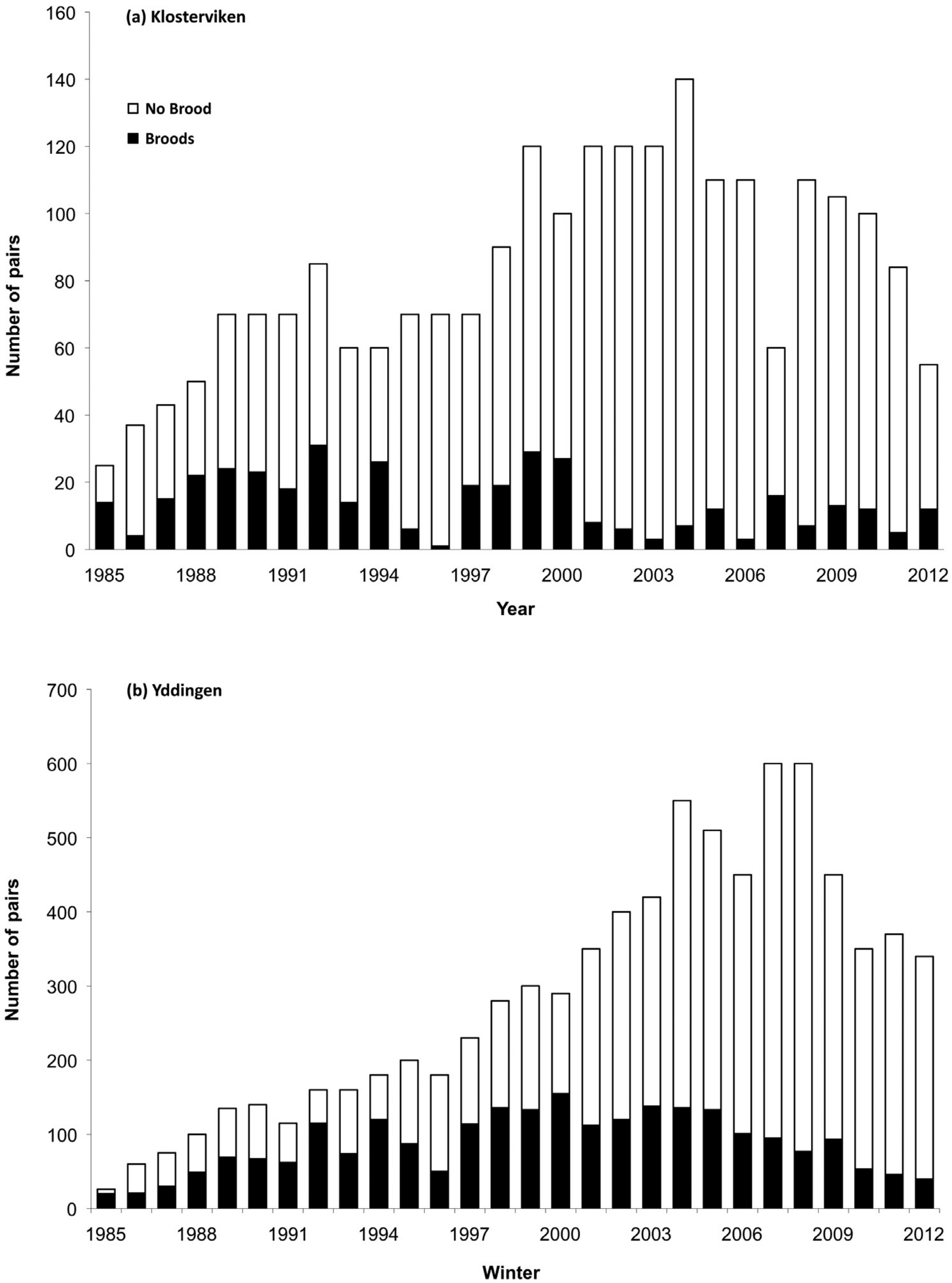

Figure 3. Total number of pairs seen with (filled bars) and without (open bars) broods in the two main study lakes in southernmost Sweden, 1985–2012.

increasing to a peak of 140 in 2004, after which numbers also declined. During the first years of the study, a relatively high proportion of the pairs seen at each of the two lakes produced a brood of newly hatched young, but this proportion decreased markedly during the latter part of the study period. The trend in the

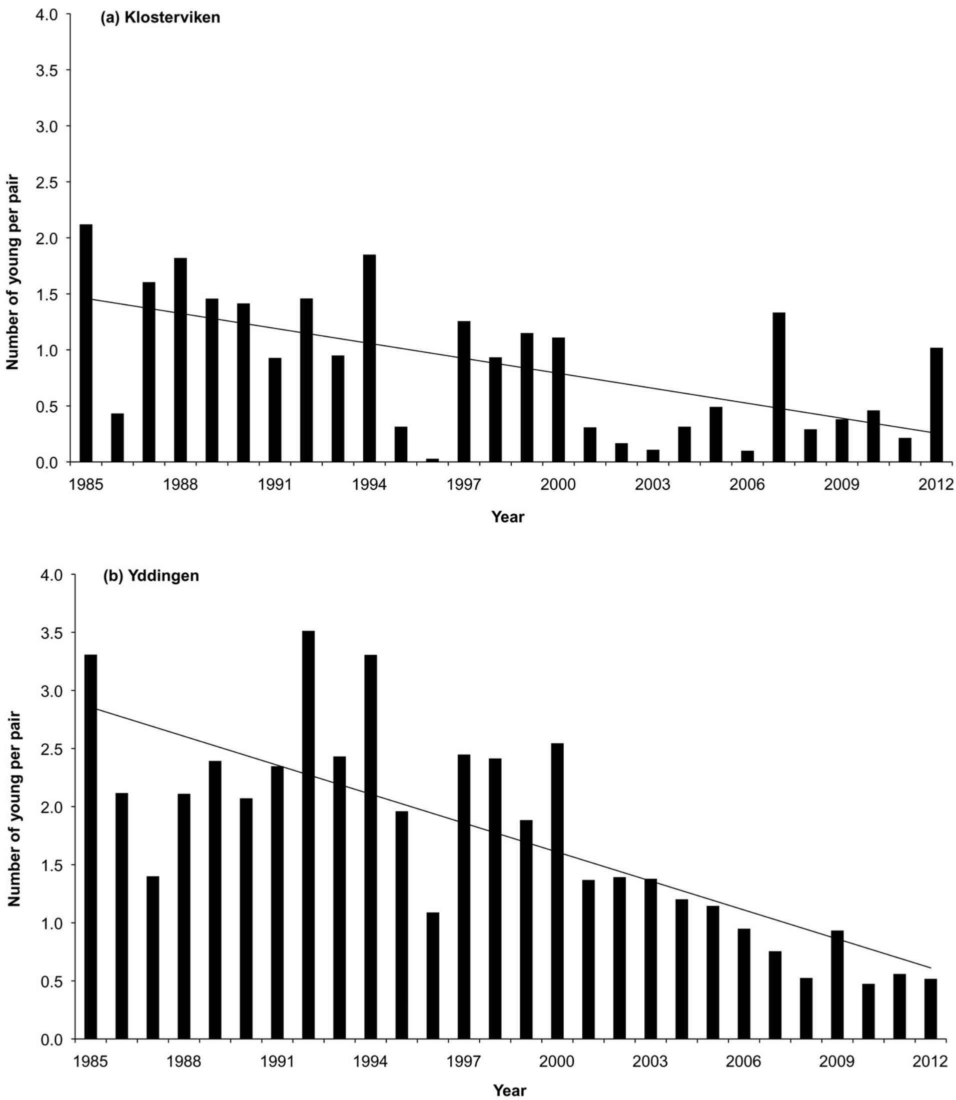

Figure 4. Number of young per pair (calculated as total number of young/total number of pairs) for (a) Lake Klosterviken (Linear regression: r = r = –0.65, d.f. = 27, P <0.01) and (b) Lake Yddingen (Linear regression r = –0.73, d.f. = 27, P <0.001) in years 1985–2012.

proportion of pairs that produced a brood decreased significantly over the study period at both lakes (Linear regression: $r_{27} = -0.73$, $P < 0.001$, for Yddingen; $r = -0.65$, d.f. = 27, $P < 0.01$ for Klosterviiken; Fig. 4). The proportion of pairs producing young varied markedly between years but generally the proportion of pairs producing a brood of small young was higher at Lake Yddingen (mean ± s.e. = 37.9 ± 3.42) than at Lake Klosterviken (20.3 ± 2.78) (Paired *t*-test: $t_{27} = 1.70$, $P < 0.001$). In some years, the population approached total breeding failure at Lake Klosterviken, but this never happened at Lake Yddingen (Fig. 4). In 1996, productivity was low in both lakes (Fig. 4), the effect also being evident among marked pairs. At Lake Yddingen, the number of broods of small young increased during the first years of the study, coinciding with an increase in the number of pairs at the site. When the number of pairs reached *c*. 300 in 1999 there was a clear levelling off in the number of broods with small young at *c*. 130–155 broods, this probably representing the limit in capacity of the feeding areas (Fig. 3, Fig. 5). At Lake Klosterviken the same initial increase in the number of broods with increasing number of pairs was followed by a decrease from 1992 onwards (Fig. 3) but there was no overall trend in the number of broods in relation to the number of pairs present on Lake Klosterviken (Fig. 5).

The presence of marked Greylag Geese breeding at the study lakes makes it possible to establish the productivity of young for individual pairs. For Lake Yddingen the number of newly-hatched young showed a slightly decreasing trend as the number of breeding pairs increased (Fig. 6); the changes were small but significant (Linear regression: $r_{21} = -0.48$, $P < 0.05$). At Lake Klosterviken, there was no significant trend over time, only marked variation between years (Linear regression: $r_{18} = 0.22$, $P = 0.37$, n.s.; Fig. 6).

The fledging success for young with marked parents ranged from 64–91% at Lake Yddingen and from 48–94% at Lake Klosterviken. There was a slightly decreasing trend in fledging rate with an increase in breeding numbers at Lake Yddingen from 1986–2006 (Linear regression: $r = -0.58$, d.f.= 19, $P = 0.05$), but no clear association between fledging success and the number of breeding pairs for a shorter time period (1987–2000) in which sufficient data were available at Lake Klosterviken (Linear regression: $r_{11} = -0.40$, $P = 0.17$, n.s.; Fig. 7).

Discussion

The data presented here supports the hypothesis that breeding density is influencing the total production by Greylag Geese at the two most intensively studied lakes in the study area. On comparing the data obtained for all Greylag Geese present at these two lakes with data from the neck-banded pairs, it appears that the density effects mostly resulted from a smaller proportion of the pairs producing a brood of newly-hatched young and not so much to a reduction in the brood size of pairs that managed to produce young. There was however a small decrease in the brood size (of small young) with an increase in the number of breeding pairs at Lake Yddingen, and also a slightly decreasing trend in the fledging rate for the goslings of marked pairs on this lake.

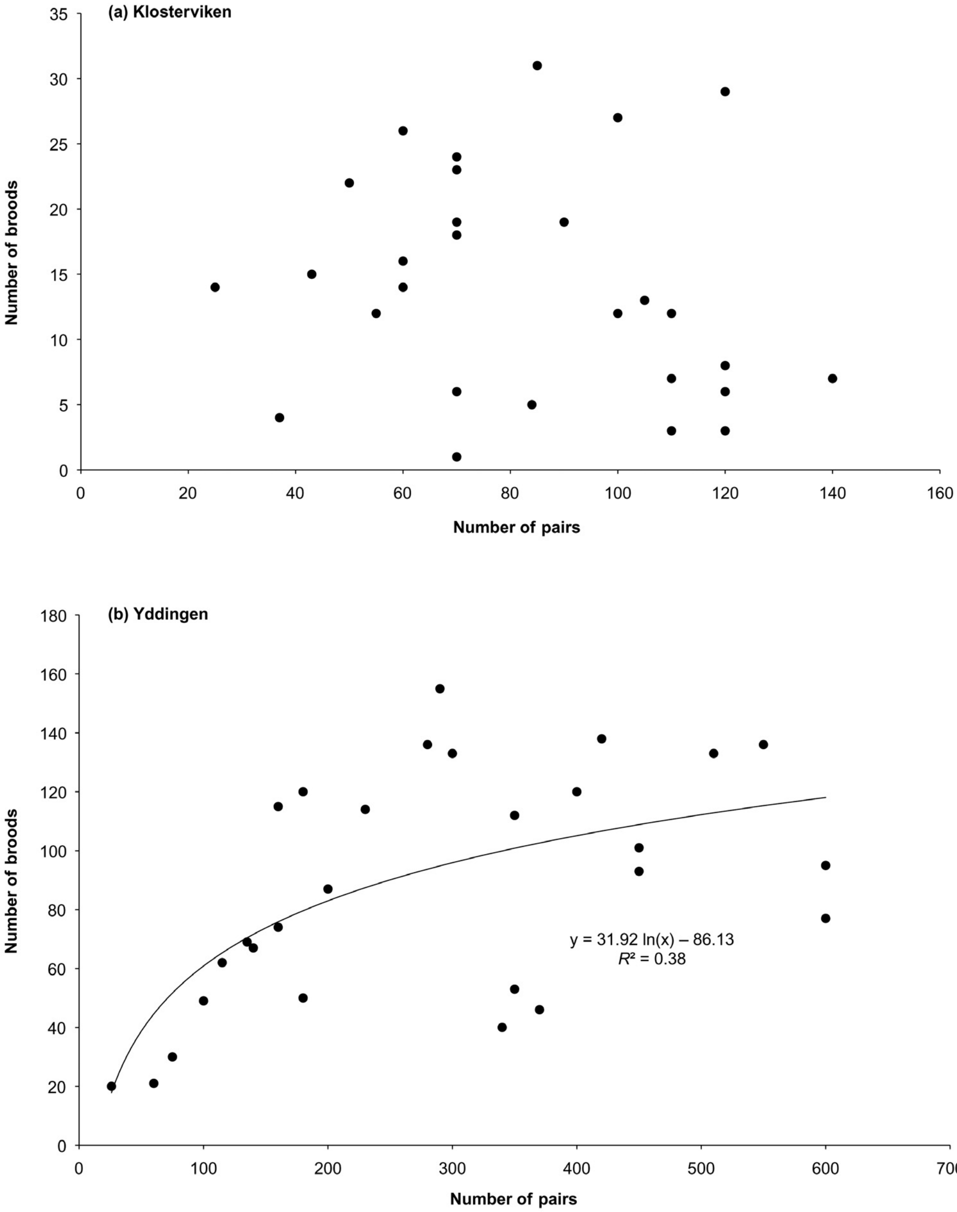

Figure 5. Number of broods of Greylag Geese with small young seen at (a) Lake Klosterviken and (b) Lake Yddingen in relation to the number of pairs recorded at the lake.

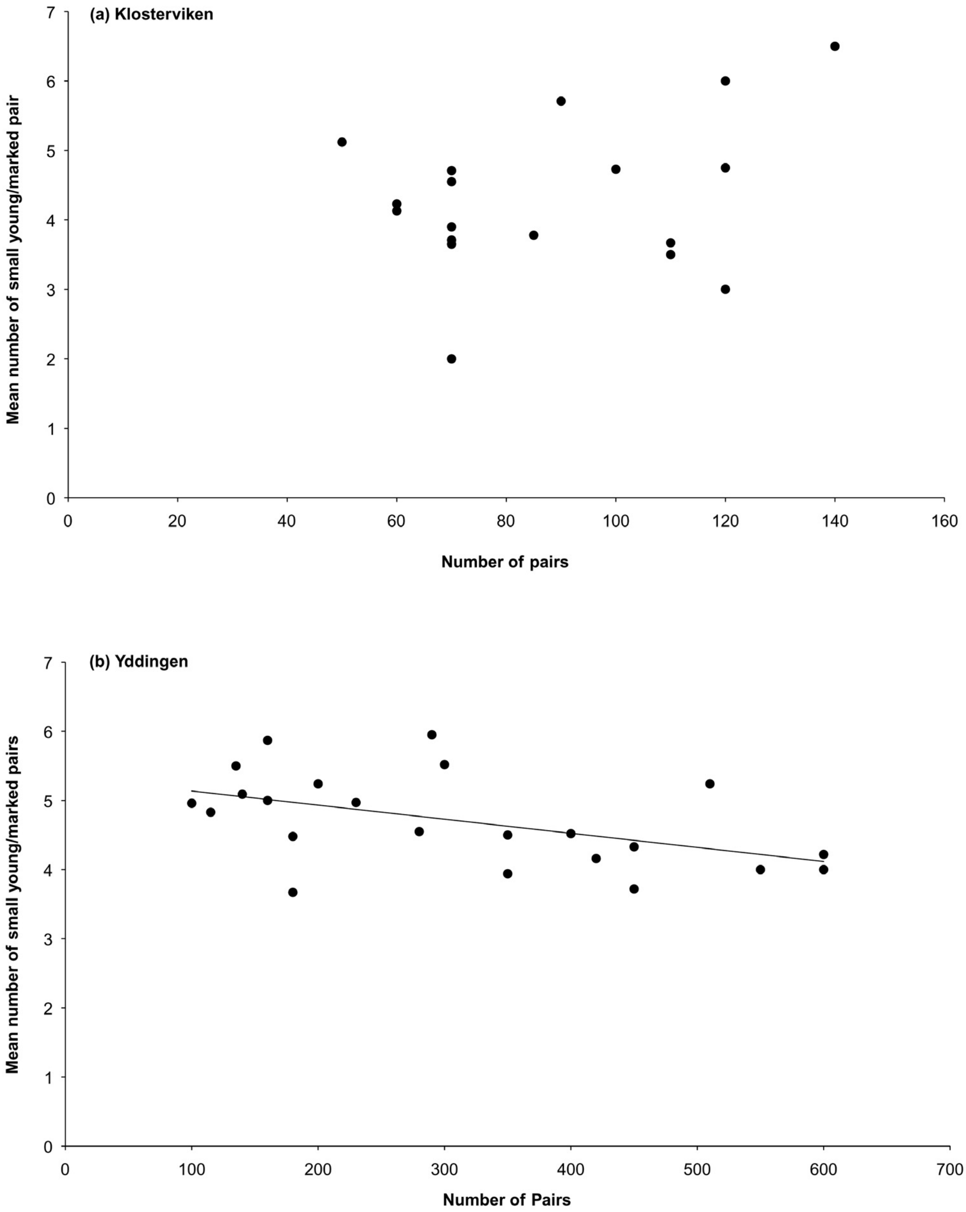

Figure 6. Mean number of small young per marked pair of Greylag Geese in relation to the number of breeding pairs at (a) Lake Klosterviken in years 1988–2006 (Linear regression: r = 0.22, d.f. =18, P = 0.37, n.s.) and (b) Lake Yddingen from 1988–2010 (Linear regression: r = –0.48, d.f. = 21, P < 0.05), in years 1988–2010.

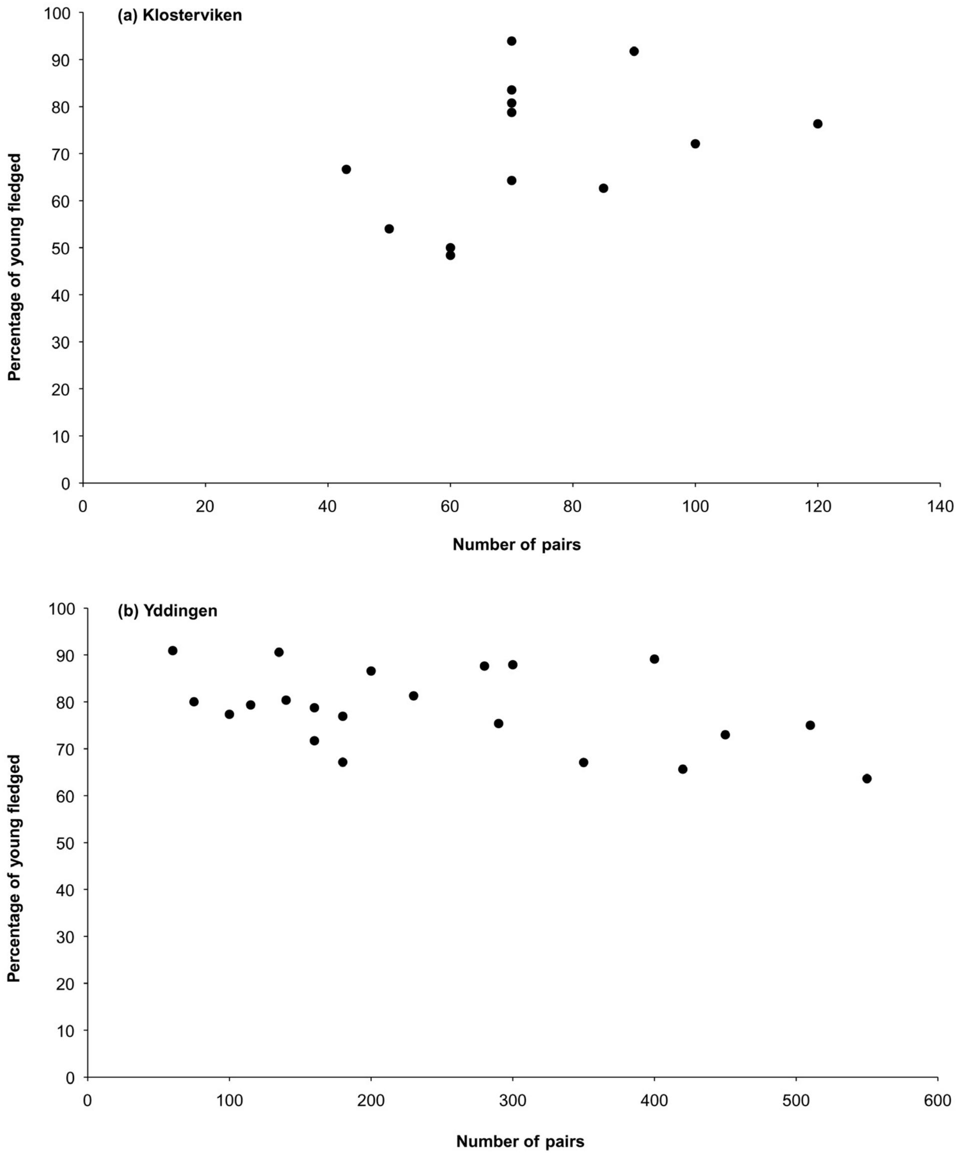

Figure 7. Survival to fledging of small young of Greylag Geese in families with marked parents (*i.e.* where individual broods could be followed) in relation to the number of breeding pairs at (a) Lake Klosterviken in years 1987–2000 (Linear regression: $r = -0.40$, d.f. = 11, $P = 0.17$, n.s.) and at (b) Lake Yddingen from 1986–2006 (Linear regression: $r = -0.58$, d.f. = 19, $P = 0.05$). The survival rate was calculated as the total number of fledged young each year, measured as a percent of the total of newly-hatched young for all marked pairs at each lake, for years in which data were available on both the number of newly-hatched young and of fledged young at each site.

In a separate analysis of the survival of the Greylag Geese from southwest Sweden in 1985–2005, Pistorius *et al.* (2007) found no evidence for a decrease in the first year survival of neck-banded yearlings from the study area; indeed, survival rates were higher in the second part of the study period than in the first. For adult Greylag Geese marked in southwest Sweden, there was no trend in the annual survival rates over time (Pistorius *et al.* 2007).

There was a time-lag between the decline in productivity and the more recent decrease in the number of pairs recorded at both the study lakes. This was *c.* 7–8 years at Lake Klosterviken (a decline in numbers of pairs from 2008 and in productivity from 2001) and 3 years at Lake Yddingen (with a decline in numbers of pairs from 2008 and in productivity from 2005). This delay may be associated with the high level of site fidelity by the females (Nilsson & Persson 2001a) and their relatively long life-span (Pistorius *et al.* 2007). Resighting data showed that females did not change breeding lake even if they experienced poor breeding success over several years (Nilsson & Persson 2001a).

There were clear differences between the two study lakes despite both showing a reduction in productivity in relation to the increase in the number of breeding pairs. The production of young and the survival of the young was better for goslings hatched at Lake Yddingen than at Lake Klosterviken, and this led in due course to higher recruitment into the breeding population of geese with Lake Yddingen as their natal area (Nilsson & Persson 1994; Nilsson *et al.* 1997, 2002). The effect of density on the proportion of pairs producing a brood of newly-hatched young was also seen earlier at Lake Klosterviken than at Lake Yddingen (Nilsson *et al.* 2002) with this being evident during 1995–2000 at Lake Klosterviken, whereas no such effects were found at Lake Yddingen until 2000 onwards (Fig. 3, Fig. 4). The differences between the two lakes most likely result from differences in the extent and quality of feeding habitat available to the geese, as discussed by Nilsson *et al.* (2002).

It is important to remember that, in addition to the effects of local breeding density on the annual production of young at the two study lakes, other factors could contribute to the falling level of reproductive success. These include the choice of winter areas, timing of arrival in spring, age of the birds and annual variation in the feeding conditions available to the young. For instance, there were unusually hard winters in two of the years before the decline, and the fewer offspring in these years could potentially be related to conditions at the winter sites (*cf.* Nilsson & Persson 1996).

Against these results from just one important breeding area, it is of interest to note that the steady increase in the national September counts of Greylag Geese in southern Sweden seems to have levelled off after a peak of 227,000 birds in 2009 (Nilsson 2013). The number of Greylag Geese staging in Sweden had increased ten-fold since the autumn counts commenced in 1984 up to 2009 (Nilsson 2013; Nilsson & Haas 2015), but there has been a quite marked decrease in the September totals in very recent years. It is important to remember, however, there has also been increased hunting pressure on the species in recent times. The latest count (2015) was again relatively high, with more than 200,000 Greylags recorded in Sweden (L. Nilsson, unpubl. data).

In North America, large increases in goose species such as the Lesser Snow Goose *Chen caerulescens caerulescens* and Ross's Goose *Chen rossii* have affected the arctic ecosystems because of the herbivory of the geese on the breeding grounds, leading to some populations showing density-dependence in recruitment through declines in local food availability (Traylor *et al.* 2012). Density-dependent effects have also been recorded for a temperate breeding population of Canada Geese in North America (Lebeuf & Giroux 2014), where breeding success was affected by different factors related to the local population density, including an increased level of interference and aggressive interactions between neighbours in a dense population (Giroux 1981). Another possible influence discussed by Lebeuf & Giroux (2014), was that in dense populations some pairs may be forced to nest in inferior cover or in other situations where they were more easily predated (see also Rodenhouse *et al.* 1997, 2003). This factor could be of importance in the present study because increased density among the breeding Greylag Goose pairs mostly affected the proportion seen with a brood of small young (which may reflect levels of nest predation, or competition between pairs), whereas the brood sizes at hatching did not show any marked changes over the years.

Density-dependent effects in increasing populations have also been found in waterfowl other than geese. Nummi & Saari (2003) noted a decrease in productivity in an increasing population of Mute Swans *Cygnus olor*. The question of density-dependence in breeding ducks has been addressed in several studies, the issue being of great interest in the discussion of the regulation of the harvest of waterfowl in North America (see Burnham & Andersson 1984). The relevant literature on possible density dependent effects in ducks has been reviewed recently by Gunnarsson *et al.* (2013). They found density-dependence in a number of duck species affecting many different stages during the breeding cycle, although they also reviewed a number of studies that found no such evidence. Hence, there remain many unresolved questions in relation to the existence, nature and strength of density-dependence in Greylag Goose populations, which should be answered to inform decisions about the future management of these populations.

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Photograph: Greylag Geese with brood at the Lake Yddingen study area, Sweden, by Leif Nilsson.

