Egyptian Goose *Alopochen aegyptiaca*: an introduced species spreading in and from the Netherlands

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Abstract

The Egyptian Goose *Alopochen aegyptiaca* was introduced as an ornamental species to parks in the Netherlands during the 20th century because of its exotic plumage. Escaped birds started to breed in the wild in 1967, and the species has now colonised most of the country. From the 1980s onwards the birds spread further to Germany, then to Denmark, while escapes from parks in Brussels established viable populations there and in France. This study summarises the latest available information on the numbers and distribution of free-living Egyptian Geese in the Netherlands and Europe. The population dynamics of the species were analysed to provide a better understanding of the development of the Dutch population over the past 40+ years, with special attention paid to the effects of culling, natural winter mortality and possible habitat preferences. Numbers breeding in the Netherlands were estimated at *c*. 10,000 pairs in 2010, and the total population at *c*. 45,000 individuals in winter 2010/11. Both breeding and non-breeding numbers increased exponentially (by 28% annually) from the establishment in the wild until 1999. However, the rate of increase has slowed in the last ten years, likely due to saturation of available breeding sites and an increase in culling activity. Within-season mortality in severe winters exceeded that during mild winters. The success of the Egyptian Goose in the Netherlands can likely be attributed to the abundance of freshwater areas available close to grasslands with few trees. Extrapolation up to 2010 of trends observed in Belgium and Germany until 2005 and 2006, respectively, suggests that these breeding populations together exceed 16,000 pairs, bringing the total numbers breeding in northwest Europe (including pairs in Britain, France and Denmark) to > 26,000 pairs.

Key words: exotic, feral, introduced, non-native, population dynamics.

The establishment and spread of alien introduced species often raises considerable public concern (Duncan *et al.* 2003). This mostly relates to potential ecological effects, such as hybridization with native species, or competition for breeding sites and limited food resources (Weller 1969). Lately, however, economic impacts including damage to agricultural crops (Conover 2002; Mangnall & Crowe 2002), social issues (*e.g.* defecating in recreational waters) and amenity effects (*e.g.* defecation in public areas) have all become matters of extensive public debate (Bomford 2003; Banks *et al.* 2008). A better understanding of the ecology and population dynamics of introduced species therefore is required to better support public discussion and provide adequate evidence upon which to base decision-making.

The Egyptian Goose *Alopochen aegyptiaca* is one of the non-native waterfowl species most rapidly spreading in Europe. It is widespread in its native range in Africa, south of the Sahara, numbering > 500,000 individuals (Brown *et al.* 1982; Banks *et al.* 2008). The species was introduced to England as an ornamental waterbird in the 17th century, and developed into a free-living, self-sustaining population in East Anglia, but has shown little growth in numbers in Britain over the centuries (Sutherland & Allport 1991).

In the second half of the 20th century, the species was kept in captivity at sites across Europe, including the Netherlands. Escaped individuals from parks in The Hague were reported breeding freely for the first time in 1967 (Teixeira 1979). Since then, the introduced population of Egyptian Geese has expanded and colonised all parts of the Netherlands (Lensink 1999a). During the compilation of the Dutch breeding bird atlas in 1999/2000, > 4,900 pairs were estimated breeding across 61% of the 1,674 atlas squares (5 × 5 km) monitored during the survey (Lensink 2002). From the 1980s onwards, the species has spread deep into Germany, with increasing numbers also reported from Switzerland and Denmark (Banks *et al.* 2008). Birds escaped from parks in Brussels in Belgium to establish another population, now spreading into France (Fouque *et al.* 2011), are perhaps supplemented by local escapes in both countries.

In contrast to the relatively slow growth of the English population since its establishment more than 300 years ago, rapid growth occurred on mainland Europe immediately after first breeding in the wild. Insight into the ecology of the Egyptian Goose is required, however, to ensure that models developed to predict future trends in the European population are scientifically sound (Kampe-Persson 2010; Rehfisch *et al.* 2010). We here present results of a study of the changes in distribution and abundance, habitat selection and winter mortality of the species in the Netherlands (the main source of the Northwest European population), to better understand the population dynamics of the Egyptian Goose in Europe and to predict its future distribution and abundance. Additionally, the current distribution and numbers of the Egyptian Goose in Europe are summarised and the possible ecological, economic and social impacts of the species are discussed.

Methods

Data

Numbers, trends and distribution of the Egyptian Goose in the Netherlands originate from data provided by the Dutch Centre for Field Ornithology (SOVON) based on observations recorded during:

1) the Dutch Breeding Bird Monitoring Project (BMP) from 1990–2009, 2) the Waterbird Monitoring Scheme (WAVO) from 1975–2008, and 3) the seven nationwide breeding pairs censuses of the period 1967–1999/2000 (in 1967, 1972, 1977, 1983, 1989, 1994, and 1999/2000).

The BMP survey in the Netherlands is designed to track trends in breeding bird numbers, based on intensive mapping of breeding bird territories. Between March and July, approximately 1,500 study plots (varying in size from *c.* 10–250 ha) are visited 5–10 times, depending on the type of habitat and species coverage, and all birds showing territorial or nesting behaviour are recorded (van Dijk 1993). Since the study plots do not reach 100% coverage nationally, SOVON presents annual changes in indices relative to the baseline year of 1990, estimated using log-linear Poisson regression models of time series corrected for missing data (Pannekoek & van Strien 2005). For our study, BMP data was available as totals for the Netherlands, and also separately for the 12 provinces and 13 different physical-geographical regions, for the period 1990–2008.

The WAVO censuses are carried out monthly from September to April at 86 important wetlands in the Netherlands, as well as at the staging sites of geese and swans (van Roomen *et al.* 2003). The counts are reported as monthly averages, and not as indices as in the BMP. Counts are carried out during daytime, and hence when Egyptian geese are at the foraging sites. Birds are only counted if present within the habitat (*i.e.* excluding birds flying over). Data from the Waterbird Monitoring Scheme was available for the period 1975–2008. During the regular WAVO survey in mid-January (which also provides the Netherlands counts for the International Waterbird Census (IWC) coordinated by Wetlands International), many additional canals and smaller waterbodies are visited, bringing the total size of the census area to approximately 1.95 million ha. Areas with missing counts are imputed by standardized methods (van Roomen *et al.* 2003), providing a robust and reliable estimate of waterbird numbers in the Netherlands. These data were available as totals and also separately for 16 physical-geographical regions.

The breeding pairs census of 1999/2000 provided the most recent nationwide count of the number of Egyptian Goose breeding pairs. For this census, the Netherlands was subdivided in 1,674 atlas squares (5 × 5 km), which all contained 25 kilometre squares. The goals of the census were to compile a list of breeding bird species and to estimate the number of breeding pairs per atlas square. All landscape types within an atlas square were visited several times during the breeding season. If breeding density was high, often only part of the atlas square was visited and the number of breeding pairs counted there was extrapolated proportionally to the amount of available habitats in the rest of the square. Like the WAVO censuses, breeding pairs census data were available for 16 physical-geographical regions.

Information on Egyptian Goose numbers outside the Netherlands was collected by personal communication with local experts and from published sources on the breeding population in Belgium (Devillers 1988; Anselin & Devos 1994;

Lensink 1999a; Banks *et al.* 2008) and Germany (Lensink 1996; Lensink 1998; Hüppeler 2000; Südbeck *et al.* 2007; Banks *et al.* 2008). The most recent data for Belgium and Germany were from 2005 and 2006, respectively.

Analysis

Population growth rates for Egyptian Geese in the Netherlands were calculated by taking the exponential of the slope of the natural log-transformed numbers plotted per year. The estimated number of breeding pairs in 2010 was calculated in two ways, both using the number of pairs reported in the Dutch breeding bird atlas as a starting point (SOVON 2002). This was the most recent complete nationwide census of breeding Egyptian Goose pairs, estimated as 4,950 pairs in 1999–2000 (Lensink 2002). One estimate for 2010 was based on the mean growth rate recorded per province by the BMP surveys in the period 2000–2009. These growth rates were applied per province, and were relative to the number of breeding pairs registered during the first year of the period (year 2000). The other method was also based on numbers registered in each province in 2000, but relied on the mean annual increase (*i.e.* 8.8% for the whole country) in bird numbers recorded by the WAVO censuses in the period 2000–2008. This growth rate was applied per province, and again relative to the numbers registered during the first year of the period (year 2000).

An estimate of the total population size (including both breeding and non-breeding birds) in the summer of 2010 was derived from the estimated number of breeding pairs. The estimate was based on Leslie matrix calculations (Caswell 2001), assuming that breeding commences after the first winter, a juvenile survival rate of 72%, adult survival of 83% and a production of 1.9 juveniles/pair/year (Table 1; values taken from Lensink 1998). However, the national database of the Royal Netherlands Shooting Association (Koninklijke Nederlandse Jagers Vereniging) shows that culling since the 1990s gradually increased to 20,000 Egyptian Geese shot in 2008, roughly equal to 1.5 geese per 100 ha, a removal of birds that has remained relatively stable since then (Montizaan & Siebenga 2010). In order to the test the effect of culling on growth rates, the model was run both with and without controlling for culling. In the former, the number of shot birds was corrected per age-class for the number of birds that would not have survived until next year.

The WAVO census data were used to test the effects of winter severity on Egyptian Goose numbers within and between years. IJnsen indices provided a measure for winter severity. This measure is the degree-sum, on a scale of 0–100, of the number of

Table 1. Leslie matrix of the vital population parameters used to model the effect of shooting on Egyptian Geese in the Netherlands.

	1st year	≥ 2nd year
Fecundity	0	0.684
Survival to 2nd year	0.720	0
Survival to > 2nd year	0	0.830

frost days (minimum temperature < 0°C), ice days (maximum temperature < 0°C) and very cold days (minimum temperature < –10°C) between November and March (Van Engelen *et al.* 2001). The IJnsen indices were used as the independent variable in a linear regression model to predict changes in the annual average number of birds counted in the winter half-year (November–March) during the years 1975–2008. A one-way ANOVA tested whether the annual changes in numbers differed significantly after severe winters (with an IJnsen index of > 30; $n = 7$), compared to after mild winters (with an IJnsen index of < 10; $n = 15$). In addition, an ANOVA assessed within-winter mortality by testing whether the difference between the average numbers of individuals counted during the waterfowl censuses in November–December and January–February were lower in severe than in mild winters. These periods are known to achieve the most extensive census coverage with the fewest imputed numbers for missing counts. Values were natural log-transformed to achieve normality.

In order to test statistically for changes in distribution, the count areas of the IWCs conducted in January each year were grouped into 16 different physical-geographical regions. Numbers counted in January 2000 and January 2008 were log-transformed and were subjected to simple linear correlation.

The habitat preference analysis relied on the habitat type classification (*i.e.* urban areas, orchards, forests, arable land, grassland, heath, water, sandy areas, and "other" habitats) of the SOVON survey areas (n = 3,959; mean ± s.d. surface area = 587 ± 955 ha) of the IWC January 2000 census. SOVON reports bird numbers per survey area but not specifically per habitat type within the area. Nevertheless, the number of Egyptian Geese varied greatly among survey areas (range = 0–299 birds). On omitting survey areas without Egyptian Geese, the mean number recorded was 12.1 birds per survey area. In order to compare the habitat types between preferred and non-preferred areas, survey areas were selected where no Egyptian Geese were observed and also where > 50 birds were observed. The surface areas of the nine habitat types were summed for these two groups. Subsequently, the arcsine transformed proportions of the habitat types within one group were compared with a paired t-test for unequal variances with the corresponding proportions of the other group.

Population growth rates outside the Netherlands were based on published data related to the breeding population in Belgium and Germany. The numbers of breeding pairs were natural log-transformed and exponential curves were fitted to the relationship between these and the year of observation. The resulting equations were then used to extrapolate the figures for Belgium and Germany up to 2010 which, when combined with data from other countries, provided a recent estimate of the total European population.

Results

Numbers in the Netherlands

Relating the most recent complete estimate of Egyptian Geese breeding in the Netherlands (4,944 breeding pairs in 1999–2000; Lensink 2002) to earlier nationwide breeding pair censuses undertaken since 1967 (reported in Lensink 1996, 2002; Table 2) gave a mean annual growth rate of 28.2% of the breeding population calculated over the whole period between 1967 and 1999. Nevertheless, the growth was not constant. The nationwide censuses and the breeding bird surveys provided similar estimates of mean annual rates of increase (*i.e.* 12.1% and 12.7%, respectively) in the period of 1990–1999 (BMP surveys were available only from 1990 onwards) but the values were lower than over the whole period, suggesting a slower growth rate during the 1990s. The increase in the number of Egyptian Goose pairs (N_{NL}) with year (t) in the period 1967–2000 could be best described by an exponential function ($\ln N_{NL} = 0.25t - 488$, $r^2_5 = 0.98$, $P < 0.0001$). Fitting a second order polynomial did not improve the relationship as the quadratic term remained 0.

There were no nationwide censuses of Egyptian Geese carried out after 1999–2000, but the BMP surveys indicated that the rate of increase slowed down further between 2000 and 2009 to an annual mean of 7.0% for the total Dutch population. The WAVO surveys (conducted between November and April) found a similar growth rate (8.8%) for the period 2000–2008. The BMP surveys also allowed an analysis at the level of the 12 Dutch provinces and 13 physical-geographical regions. The BMP surveys revealed a low growth rate of the number of breeding pairs in nine provinces, and a growth rate of > 10% in only three provinces during the period 2000–2009 (Table 2). The comparison of the growth rate of the number of breeding pairs between the periods 2000–2009 and 1990–1999, revealed a slower growth rate after 2000 in all provinces. At the scale of the 13 physical-geographical regions, slower growth rates occurred in eight, comparable growth rates were observed in two others and a higher rate only in three cases: 1) in dunes and tidal areas at the Wadden Sea islands, and the northern marine clay salt marshes; 2) higher sandy areas in the north of the Netherlands and 3) higher sandy areas in the middle and southern part of the country. A paired t-test analysis comparing the slopes of the growth rates in the 13 regions revealed a significantly lower increase in the last decade ($t_{11} = 2.48$, $P < 0.05$).

Based on the growth rate obtained per province from the BMP indices, the total size of breeding population in the 12 provinces was estimated at 10,171 breeding pairs in 2010 (Estimate 1 in Table 2). The WAVO surveys indicated a nationwide average annual growth rate of 8.8% between 2000 and 2008. Estimate 2 for 2010 in Table 2 is the product of extrapolating the number of breeding pairs recorded in 2000 per province by this value, resulting in numbers similar to Estimate 1. From Estimate 1 (10,171 breeding pairs), the Leslie matrix predicted the total population in the Netherlands (inclusive of breeding and non-breeding individuals and an ongoing culling of 20,000 individuals annually) at 45,523 birds in 2010 (Fig. 1a). Without accounting for culling, the growth of the population would have remained exponential, and the size of the population could have reached a theoretical maximum of 66,359 breeding pairs (Fig. 1b) or a total

Table 2. Number of breeding pairs per province in the period 1967–2000 (data from nationwide breeding censuses reported in Lensink 1996, 2002) and an estimate of the number of breeding pairs in the Netherlands in 2010. The rate of increase for the period 2000–2009 is derived from the breeding bird census (BMP). These rates provided Estimate 1 for 2010, whereas Estimate 2 is derived from the increase recorded by the waterfowl censuses (WAVO) during the period 2000–2008 (*i.e.* 8.8% per year at the national scale).

	Nationwide breeding pairs censuses							BMP growth rate (%/year)	Estimate 1	Estimate 2
	1967	**1972**	**1977**	**1983**	**1989**	**1994**	**1999–2000**	**2000–2009**	**2010**	**2010**
Groningen	0	0	0	0	10	28	133	10.3	355	308
Friesland	0	0	0	0	2	55	359	4.9	580	830
Drenthe	0	0	0	1	11	46	265	14.9	1,063	612
Overijssel	0	0	0	4	16	105	534	4.8	853	1,233
Gelderland	0	0	2	15	70	365	815	4.0	1,206	1,883
Utrecht	0	0	0	5	27	104	326	6.7	624	754
Flevoland	0	0	0	0	1	6	43	8.8	99	98
Noord Holland	0	0	3	16	59	190	620	11.8	1,890	1,431
Zuid Holland	1	7	43	72	128	290	891	6.4	1,656	2,058
Zeeland	0	0	0	0	1	10	119	5.0	194	275
Noord Brabant	0	0	0	2	19	60	510	7.3	1,031	1,177
Limburg	0	0	0	0	1	45	330	6.5	619	762
Netherlands	1	7	48	115	345	1,345	4,945	7.0	10,171	11,421

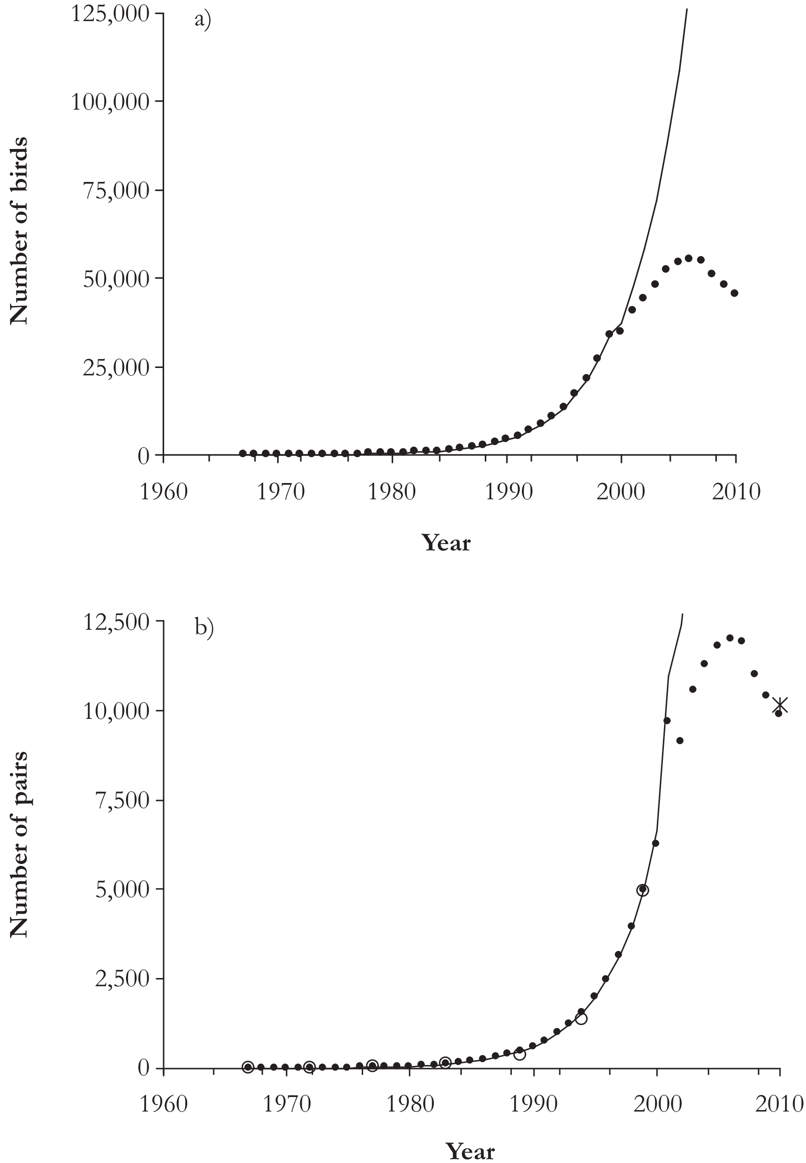

Figure 1. Modelled population development of the Egyptian Goose in the Netherlands since 1967, accounted for culling (filled dots) or not (solid line). The model was based on Leslie-matrix calculations (*cf.* Caswell 2001 with parameters from Lensink 1998). a) presents the modelled total number of birds; b) presents the modelled number of breeding pairs, the observed number of breeding pairs in the period 1967–2000 (open dots = data from Lensink 1996, 2002), and the estimated number of breeding pairs in 2010 (asterisk = data from this study; see Estimate 1 in Table 2).

population of 306,097 birds (assuming no effects of habitat limitation or other density dependent factors; Fig. 1a).

The within-year variation in the WAVO counts showed that the highest numbers were counted in September (*i.e.* after the end of the breeding season), followed by a sharp decreasing trend until January, and thereafter remaining roughly stable or slightly decreasing until March. There was no clear effect of winter severity (determined by IJnsen indices) on annual changes in abundance (linear regression: $r^2_{21} = 0.64$, n.s.), nor when comparing changes in numbers following severe and mild winters (ANOVA: $F_{1,20} = 0.26$, n.s.). However, the within-season analysis, with winter severity as categorical factor, revealed that the number of Egyptian Geese show a significantly stronger decrease during severe winters than during mild ones (ANOVA: $F_{1,20} = 9.58$, $P < 0.01$). Based on back-transformed data, in severe winters the mean number of individuals in January–February was approximately half of that in November–December (*i.e.* 54%). In contrast, in mild winters the reduction in numbers was < 8% (Fig. 2).

Distribution in the Netherlands

Habitat preferences

The annual IWCs carried out in January showed that Egyptian Geese can be found in all parts of the Netherlands, but the largest concentrations were recorded in the lower parts of the country (generally the western and northern provinces), mostly in riparian areas, where breeding density was highest (often > 10 pairs per 100 ha). The species was absent from heavily afforested areas and areas where water bodies are lacking. However, the analysis of the nationwide waterfowl census data conducted in January 2000 revealed no significant difference between the proportions of habitat types in count areas where no Egyptian Geese were counted compared to those with > 50 birds reported ($t_8 = 0.87$, n.s.). The only notable difference existed between the proportions of grasslands and arable areas: 51% of the census areas with > 50 Egyptian Geese ($n = 35$) was grassland (total = 12,728 ha), whereas of the survey areas where the species was absent ($n = 3,364$) only 35% was grassland (Fig. 3). In contrast, the proportion of arable land constituted 29% of the survey areas where the species was absent compared with 20% of the survey areas with > 50 Egyptian Geese (in total 5,008 ha).

Changes in distribution

A comparison of the numbers counted in January 2000 (*i.e.* including adults and sub-adults; N_0) and in January 2008 (N_8) for 16 physical-geographical regions revealed that total numbers increased in all areas ($\log N_8 = 0.77 \log N_0 + 0.96$, $r^2_{15} = 0.64$, $P < 0.001$; Fig. 4 a). However, the relative abundance in the regions changed, revealed by the slope of the relationship being significantly smaller than one (0.77 ± 0.15 s.e.). This resulted from regions with larger numbers in 2000 increasing proportionally less than regions with small numbers. A similar comparison to the number of birds counted in January 2000 (N_0) per physical-geographical region and the number of breeding pairs (*i.e.* only adult birds) in 2000

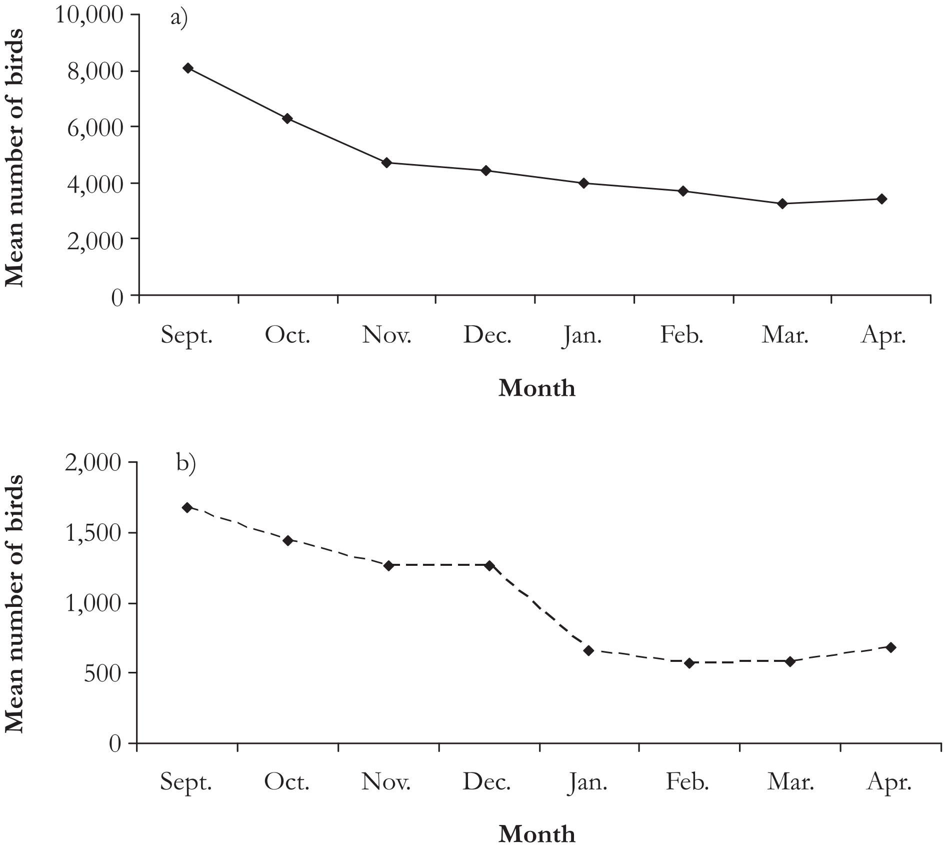

Figure 2. Mean number of Egyptian Geese per month in the winter half year during a) mild (n = 15) and b) severe winters (n = 7) during the period 1976–2008. During the last decade, when bird numbers were the highest, five mild winters but no severe winters occurred, causing generally higher mean numbers during mild winters (note the difference in the scale of the vertical axes).

(N_{0b}) in the same regions also showed a close relationship ($N_{0b} = 0.62 \log N_0 + 0.98$, $r^2_{15} = 0.80$, $P < 0.001$; Fig. 4 b).

Introduced populations elsewhere in Europe

According to the latest estimates, 700 birds breed and at least 1,000 winter in England (Rehfisch *et al.* 2010). However, due to the patchy reporting of breeding Egyptian Geese, these figures could be underestimates and the real size of the breeding population could be much higher (2,500–3,000 individuals suggested by Banks *et al.* 2008).

In Belgium, the first successful feral breeding dates from 1982 (Segers 1984; Gabriels 1985). In 2002, the number of breeding pairs was estimated at 800–1,100 (Banks *et al.* 2008), at 1,300 pairs by 2005 in

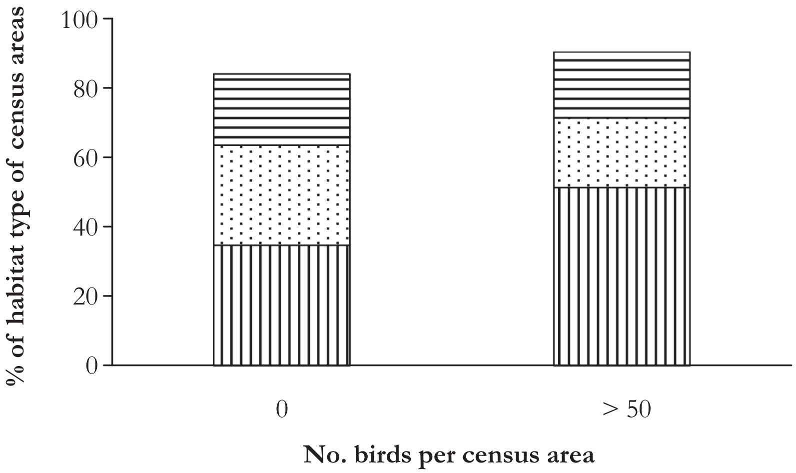

Figure 3. Proportion of the most important habitat types in waterfowl census areas where 0 (in total 3,364 areas with a surface area of 1,918,627 ha) and > 50 Egyptian Geese (in total 35 areas with a surface area of 24,866 ha) were observed in January 2000. Dotted area = arable land, vertical stripes = grassland and horizontal stripes = water. Habitat types of minor importance are omitted; hence proportions do not add up to 100%.

Flanders only (Anselin & Vermeersch 2005), and at 330–590 pairs by 2007 in Wallonia only (Jacob *et al.* in press). The population is still expanding its breeding range, especially in the western and central part of the country (Anselin *et al.* 2010). According to the latest counts, the population was estimated at around 3,000 individuals in winter 2009 (Huysentruyt *et al.* 2010). Based on available data on the breeding population in Belgium, the number of Egyptian Geese pairs (N_B) increased with year (t) on average by 35.9% between 1982 and 2005 ($\ln N_B = 0.32t - 630$, $r^2_4 = 0.95$, $P < 0.01$; Fig. 5).

In Germany, breeding of free-living birds started in 1981 along the river Rhine, originating from the introduced population in the Netherlands (Lensink 1996), building to an estimated 2,200–2,600 pairs in 2005 (Bauer & Woog 2008). Numbers in Germany (N_G), increased exponentially during 1981–2005 ($\ln N_G = 0.33t - 659$, $r^2_4 = 0.90$, $P < 0.02$; Fig. 5). By extrapolating the Belgian and German trends, the total breeding population in Belgium and Germany is estimated to have exceeded 16,000 pairs in 2010.

In France, 618 individuals were counted in 2009, with 125 breeding pairs observed in the summer (Fouque *et al.* 2011). In Denmark, at least 20 pairs were breeding in 2007 (Banks *et al.* 2008) and, according to the latest records in 2009, a total of 544 observations were listed of 1–63 individuals present throughout the year (Kampe-Persson 2010). A small number of birds occur in Switzerland; two pairs have bred in an urban park each year since 2003 (Banks *et al.* 2008), and in 2009 two new breeding sites were recorded (Verena Keller, unpubl. data).

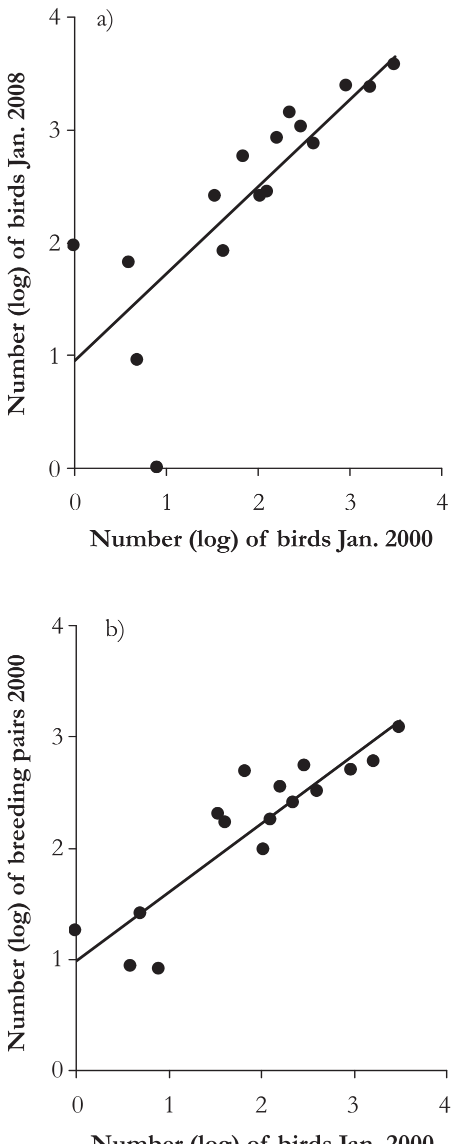

Figure 4. Comparison of the number of Egyptian Geese in: a) January 2000 and January 2008, and b) January 2000 with the number of breeding pairs in 2000 in the 16 physical-geographical regions of the Netherlands. All axes are log transformed.

Furthermore, some birds are regularly seen or occasionally known to breed in Spain, Italy, Sweden, Poland and the Czech Republic (Banks *et al.* 2008).

Discussion

The Egyptian Goose population in the Netherlands showed rapid exponential growth shortly after feral breeding was first recorded in 1967. By 2010, the breeding population was estimated at > 10,000 pairs, equivalent to over 45,000 individuals in the total mid-winter population. Breeding density was highest in riparian areas and 51% of the larger groups of Egyptian Geese were observed on grasslands in 2000. Our results suggest that the birds generally use the same habitats throughout the year. Winter severity seemed to have a negative effect on within-winter numbers. On summing the breeding pairs in the Netherlands, Belgium, Germany, Great Britain, France and Denmark we estimated the total number of breeding birds to be at least 26,000 pairs in 2010.

Despite the generally increasing trend in the Netherlands between 1967 and 2008, population growth has slowed in the past decade. In this latter period, the number of breeding pairs has increased only slightly in ten out of thirteen provinces. This could be due to increasing culling intensity, could imply that nearly all the suitable breeding sites had been occupied earlier, or be a combination of the two as a result of different factors acting locally. Up until 1994, the breeding range expanded at an average rate of 3.0 km per year (Lensink 1998), and the species was found breeding in

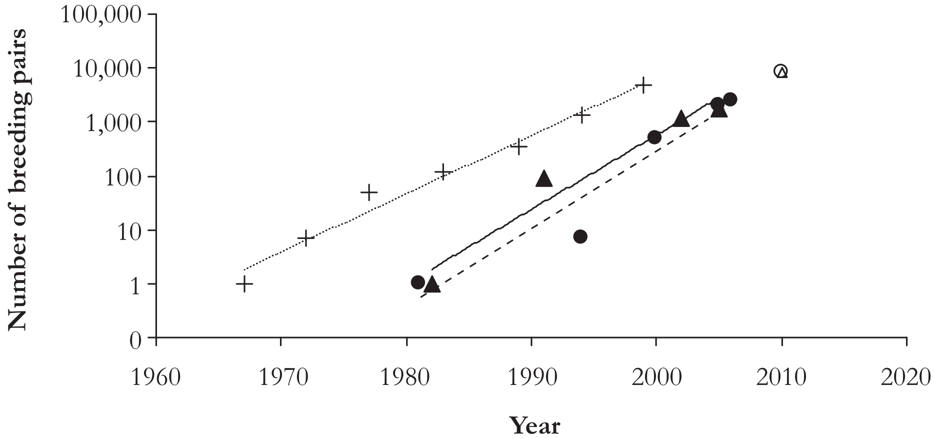

Figure 5. Growth of the Egyptian Goose population in western Europe. Filled triangles and solid line (lines are exponential trends) depict Belgium, filled dots and dashed line Germany. Open symbols indicate the extrapolated number of breeding pairs for these countries. The trend of the breeding population (based on nationwide counts) in the Netherlands between 1967 and 1999 is also provided (crosses and dotted line) for comparison. Note the log-scale of the vertical axis.

61% of the 1,674 atlas squares (5 × 5 km) in the Netherlands by 1999 (Lensink 2002). Exponential growth is frequent amongst populations of invasive species in newly colonised areas, often followed by a period of little or no increase (Lensink 1999a). In newly colonised areas, observed breeding success was much higher (60–70% of nests successful) than amongst earlier established populations (15–30% of nests successful; Lensink 1996), indicating density-dependent limitations on growth. One of the physical-geographical regions where the local population is still growing exponentially is located far from the sources of the escaped populations (*i.e.* the dunes and tidal areas of the Wadden Sea islands), whereas the other two regions provide lower quality habitats (*i.e.* sandy areas), which might reflect their lower preference by Egyptian Geese. Comparing all physical-geographical regions between 2000 and 2008 revealed that the numbers increased significantly in each of the different regions. However, the fact that the increases were greater in physical-geographical regions where numbers were relatively low in 2000, also suggests that density-dependent effects may be present.

In order to estimate the current size of the Dutch Egyptian Goose population, we relied on the observed growth rate of the breeding population (BMP indices). This trend seemed to be very similar to the one derived from nationwide censuses undertaken during the period 1990–1999, and was thus assumed to be trustworthy. In addition, estimates from the Royal Shooting Association on the size of the breeding population in each province of the Netherlands were close to the BMP estimates (Montizaan & Siebenga 2010). According to our modelled results, the size of the national population reached its maximum in 2006 at nearly 12,000 pairs, and more than 55,000 individuals in July. By assuming an annual culling of 20,000 individuals, the model predicted slightly decreasing or stagnating numbers since then. In contrast, according to the latest estimates on the number of breeding pairs in the Netherlands, the increasing trend continued until 2010 (Boele *et al.* 2012). The discrepancy may occur due to the culling figures also being estimates, and possibly varying annually. Moreover, the model relied on the assumption that the number of birds shot is equally divided among age-groups, which may not necessarily be the case. Furthermore, the parameter values on survival and reproduction originated from the early increasing phase of the population, and may be lower now through density-dependence. If so, this might also explain why the population has stabilised (even without culling). Nevertheless, the model clearly shows that without the gradually increasing culling since the 1990s the population size could have already reached 28,213 pairs, the potential maximum calculated based on the amount of suitable habitat available (SOVON unpubl. data).

Lensink (1996) reported adverse effects of winter severity on the rate of increase for the years 1975/76–1998/99. In our extended study period, such clear effects were not detected, although effects of winter severity on within-season changes in abundance were found. The species is not known to conduct regular, directed migration in the Netherlands, although smaller movements do occur outside the breeding season (Lensink 1996, 1999b). However, more dispersion could occur in severe winters. In its natural range the species moves large distances to moulting sites, and also in times of food scarcity (Del Hoyo *et al.* 1992; Maclean 1997). Moreover, recent ringing studies in the Netherlands, Belgium and Germany found that individuals of the introduced European populations also regularly disperse up to several hundred kilometres from the ringing site (Van Dijk & Majoor 2011). Nevertheless, severe winters occurred more frequently during the period 1975–1999 than in subsequent years, leading to greater winter movements, which may have caused the discrepancy in the results of this study compared with the earlier work of Lensink (1996). Alternatively, the increasing culling mortality since 1999 could have masked the effect of severe winters, or the larger population may be more capable of recovering after a severe winter by attaining higher reproductive success in the following breeding season (Lensink 1999a).

The similarity between the total numbers recorded in January 2000 and the number of breeding pairs in 2000 is striking, suggesting that the winter distribution of Egyptian Geese in the Netherlands reflects their breeding distribution. Although the species is well-known for its wide choice of breeding habitats (Harrison 1978), they mostly prefer to stay close to (< 1 km) freshwater bodies (Pitman 1963). Generally, Pleistocene soils are thought to provide lower quality breeding habitats (Lensink 2002), and in the Netherlands they breed most commonly in trees, old nests of other birds, or tree cavities (Lensink 1998). The Egyptian Goose feeds mainly on grass in the Netherlands, and areas with abundant grasslands appeared to be the preferred habitat. Our study found that the highest concentrations occurred close to water bodies in open grasslands with a few trees, which is also the typical habitat for the species in its natural range in Africa (Del Hoyo *et al.* 1992).

The population in England has grown slowly since its establishment more than 300 years ago, whereas in the Netherlands a rapid exponential growth was achieved shortly after the breeding started. Breeding success of the Egyptian Goose is low in England (1.5 fledglings per pair; Sutherland & Allport 1991), as well as in its native range (Eltringham 1974), compared with the Netherlands (4.5 fledglings per pair; Lensink 1996). Low predation pressure, and the abundantly available, fertilized grasslands adjacent to freshwaters that create outstanding habitats for herbivorous waterfowl (Van Eerden *et al.* 2005), may be the reason for the larger number of fledged chicks in the Netherlands.

The size of the Egyptian Goose population in northwest Europe has increased rapidly in the past decades and could have exceeded 26,000 breeding pairs by 2010. Supposing a similar population structure as in the Netherlands, this could translate to > 100,000 individuals including the non-breeding adults and sub-adults. Our extrapolations are based on the assumption that the rate of increase was constant until 2010. Based on the experiences in the Netherlands, and on the amount of suitable habitats in Belgium and Germany, it is not likely that the increase would have slowed since the latest published censuses. On the contrary, the species is expected to expand its breeding range further. Due to the negative effect of winter severity, the 0°C isocline could form the approximate border of the expansion range (Lensink 1998), and hence the species will likely spread mostly southwards.

The increase in abundance and distribution of such an introduced species commonly result in substantial public concern about their eventual ecological and economic impacts. Waterfowl species have a great propensity to hybridize with other species (Weller 1969). Hybridizations of Egyptian Geese mainly occur with other introduced goose and duck species (Lensink 1996; Harrop 1998; Banks *et al.* 2008), although these hybrids are usually infertile (Susanne Homma and Olaf Geiter, unpubl. data). As the birds' main food is grass, which is abundant throughout Europe, inter-specific competition for food is likely to be of minor significance. Although Egyptian Geese are often observed being aggressive towards other birds, the increasing population in the Netherlands seems not to have had a negative effect on the population development of native species so far (Lensink & van den Berk 1996). Only one study reported evidence on such an effect, where Black Sparrowhawks *Accipiter melanoleucus* raised fewer chicks due to usurpation of nests by Egyptian Geese (Curtis *et al.* 2007).

Economic impacts seem to be more profound. The increasing native population in South Africa is considered to be an agricultural pest, especially around water bodies used for moulting, where considerable damage to agricultural fields has been reported (Maclean 1993). Young wheat and barley shoots and leaves were mostly consumed, but Egyptian Geese also seem to select surface seeds (Mangnall & Crowe 2001, 2002). Egyptian Geese have likewise been reported feeding on agricultural fields in England (Sutherland & Allport 1991), the Netherlands (this study) and Belgium (Beck *et al.* 2002), although damage to crops has not yet been directly measured. Whilst a period of a few days grazing may encourage plant growth (Kear 1970), it is doubtful that this will ease the worries of European farmers when increasing numbers of Egyptian Geese appear on their land. In England, the Egyptian Goose is on the list of species that can be legally shot without a special permit (source: RSPB website). In Belgium, this holds for all exotic species, and in Germany for the period between 1 August and 15 January. Our study shows that, if necessary, such culling measures could be effective to stop or limit further growth of Egyptian Goose populations in Europe.

Acknowledgements

The study was funded by the Invasive Alien Species Team of the Netherlands Ministry of Agriculture, Nature and Food Quality. The information incorporated in this publication was first published as a Bureau Waardenburg report (nr. 10-029). The authors thank Peter van Horssen for the GIS analysis and Hans Schekkerman, Chris van Turnhout and Berend Voslamber from SOVON for their cooperation in discussions and delivering data in early stages of the work. Popko Wiersma from SOVON carried out habitat suitability index calculations. We were happy to be able to rely on data provided by A. Bloomfield, F. Majoor, B. Sage, W.R. Siegfried and D. Vangeluwe. We want to thank Anny Anselin, Vicky Knudsen, Verena Keller, Carol Fouque and Vincent Schricke for providing information on the status of Egyptian Geese elsewhere in Europe. We also thank Theo Boudewijn, Tom van der Have, Eileen Rees, Tony Fox and two anonymous reviewers for providing valuable comments on the manuscript.

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