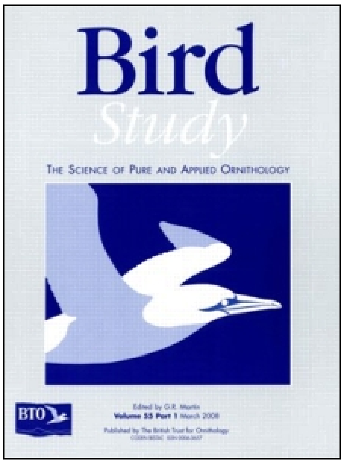

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Aspects of the biology of Egyptian Goose *Alopochen aegyptiacus* colonizing The Netherlands

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Since 1967, the Egyptian Goose has established a feral breeding population of some 1350 pairs in the Netherlands and colonized large parts of the country. Aspects of the breeding cycle and the changes in winter numbers are analysed. The Dutch population has a six-month breeding season and overall breeding success in the Netherlands is higher than in Africa, or in the British population. The proportion of successful pairs and overall breeding success decreased a few years after colonization of new areas. Timing of the onset of incubation was positively related to winter severity. Density-dependent factors appeared to begin to operate soon after colonization. As soon as the population stabilized, environmental factors became of major importance. Although population size is reduced during severe winters, the delay in the onset of breeding and relatively high success after such winters, as well as the prolonged breeding season, can quickly compensate for these losses. This combination may explain the relatively greater breeding output of this tropical species in the moderate climate of Western Europe.

The Egyptian Goose is an African species breeding south of the Sahara and in the Upper-Nile Valley.[1] In Africa, the species shows no regular migration, making irregular movements up to 1000 km in response to the alternation of wet and dry seasons.[2–4] Despite the differences in climate compared with Africa, the species shows no regular migration within Europe.[5,6]

The species was introduced to Europe more than two centuries ago as an ornamental waterbird.[7] Since the 18th century, the species has bred in the wild in Great Britain, the more or less stable population of 125 pairs centred mainly in Norfolk.[6,8] Since 1988, the numbers have increased, mainly through colonization of nearby Suffolk.[9,10]

On the continent, feral breeding was first observed near The Hague (The Netherlands) in 1967.[11] From 1969–94, the number of breeding Egyptian Geese in The Netherlands rose to 1350, colonizing many new breeding areas.[5,12] Since 1990, Dutch birds have started to colonize Germany along the rivers Rhine and Eems. In Belgium, Egyptian Geese escaped from the Royal Gardens near Brussels around 1975,[13] creating a feral population, which numbered 100–150 pairs by 1994, mainly breeding in the vicinity of Brussels and central Flanders.[14] There seems to be little exchange between the Dutch and Belgian populations, based on the relative numbers in both countries. Compared to Great Britain and Belgium, the increase in numbers in The Netherlands has been remarkably fast.

How then, has a resident tropical species managed successfully to colonize breeding grounds in temperate Europe? Why too, was the Dutch colonization so spectacular, compared with the modest recent increase in England? Several hypotheses could explain the differences in the rate of increase of feral Egyptian Goose populations: differences in breeding performance and/or differences in mortality.

Since Egyptian Geese are still colonizing The Netherlands, density-dependent factors might be expected to operate in areas where the species has already been breeding for some time. For this reason, the number of breeding pairs in fixed survey areas will be used as a

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crude index of density. The severity of the winter[15,16] is a second factor which might operate on the population of this tropical species. This could affect the overwinter survival and/or the timing and duration of the following breeding season. As part of the population is breeding in the floodplains along the rivers in The Netherlands, inundations might also influence the population dynamics of the species. When inundated, most breeding sites, as well as feeding grounds, are flooded.

MATERIALS AND METHODS

Breeding data

Breeding data were collected from the coastal dunes near the city of Leiden, and along the rivers Rhine and Waal near the borders with Germany (Fig. 1). In the dunes, most pairs occur along ditches and drains. In the river floodplains, they breed mainly along clay and sand pits.[5]

Most data on breeding performance were collected during fieldwork for the Dutch Common Breeding Bird Census (comparable with the British Common Bird Census).[17,18] Survey areas were visited about eight times every 10–14 days between late March and July.

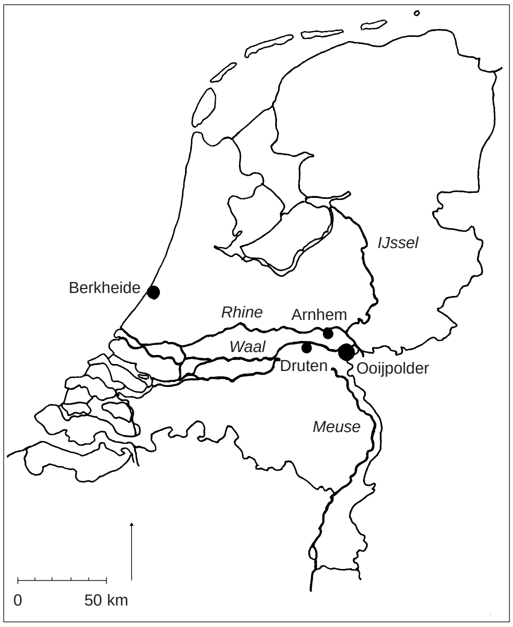

Figure 1. Map of The Netherlands showing the different survey areas and the rivers.

In most years, some additional visits were made, especially in early March, July and August. In the Berkheide (1.000 ha) and Ooijpolder (4.100 ha) survey areas, observers counted the total number of territorial pairs and the number of fledged young per successful pair, at the end of the breeding season.

For each Egyptian Goose pair, in the survey areas of Druten (369 ha) and Arnhem (220 ha), the presence and number of young were recorded during each census visit. Most pairs (75%) with young were seen during the first visit after hatching. Since parents with young do not disperse, it is assumed that all observations relate to pairs nesting within the survey areas. In most cases, this was confirmed by observations of territorial pairs during the visits before the estimated hatching date. The hatching date was estimated from the size of the young. The incubation period for the Egyptian Goose is 28–30 days.[19] Therefore, the start of breeding was calculated to be 29 days before the hatch date. Data on the onset of incubation and hatching were grouped per standard week (week 1 is 1–7 January, 2 is 8–14 January, etc.).

The fledging period is 70–75 days.[20] The average number of young was calculated for three periods: the first two weeks after hatching, week 4 and 5 together and week 8, 9 and 10 together, readily identifiable in the field. These three averages give an impression of the survival of the young up to fledging, although they may underestimate the number of young at hatching and overestimate the number fledged at the end of week 10.

In this paper, the proportion of successful pairs is expressed as the number of pairs seen with at least one (nearly) fledged young out of the total number of territorial pairs in the survey areas. Overall breeding success and the breeding success of successful pairs, both expressed as the average number of young fledged, were calculated on a similar basis.

Data on all the survey areas were used to calculate the overall breeding success. The proportion of successful pairs for the coastal dunes and the river floodplains were assessed separately. Data from Arnhem and Druten were used to analyse the length of the breeding season, the onset of hatching and breeding as well as the survival of young.

Non-breeding census data

In The Netherlands along the rivers Meuse, Rhine, Waal and IJssel (Fig. 1), wildfowl counts have been carried out on a monthly basis during the winter season since 1969. Counts were done around the 15th of each month between September and April. For this paper, the total number of Egyptian Geese along the rivers in each month was cumulatively summed to give a seasonal total. These totals are used as a population index for Egyptian Geese along the Dutch rivers.

Physical and meteorological factors

Data on the water level of the Rhine at the point where it enters The Netherlands (Lobith), were obtained from the Ministry of Public Works (Rijkswaterstaat). Most of the river floodplains along the Rhine, Waal and IJssel become inundated when the water level at Lobith is approximately 12.5 m above sea level (asl). In relation to breeding success, the number of days in the months April, May and June with water levels above inundation level, were taken.

The severity of the winter in The Netherlands is summarized in one index *V*,[21] as follows: $V = (v^2/3632) \times (y/310) \times (z/9)$, where v is the number days with frost (minimum day temperature below 0°C), y the number of 'icy days' (maximum day temperature below 0°C), and z the number of 'very cold days' (maximum day temperature below –10°C). Winters where $V > 25$ are considered severe. [21] Temperature data were obtained from the Royal Dutch Meteorological Institute (KNMI). This gave a range of values for V where < 9 is mild, 10–18 quite mild, 18–28 normal, 28–45 cold and > 45 severe.

RESULTS

Population expansion

Since initial colonization, the Dutch Egyptian Goose population increased exponentially during which time it spread to colonize new areas along the rivers IJssel, Waal and Meuse.[5,12] At the local scale, the number of breeding pairs showed an exponential increase during the early years, followed by a period of little or no increase, as in the survey area of Berkheide where numbers started to fluctuate after 1984[22] and in the Ooijpolder from 1991 onwards[23] (Fig. 2). For both areas, this is supported by a negative correlation between the population size and the relative increase in years (Berkheide $r = 0.694$, df = 17, $P < 0.01$; Ooijpolder $r = 0.591$, df = 15, $P < 0.05$, 1987 excluded because of a strong decline after a severe winter). In both areas, the first years after colonization started were characterized by a relatively rapid increase, as were the years after a sharp decline (Ooijpolder 1988, Berkheide 1984, 1992), the following years by a slower increase, and most of the recent years by a slight decrease.

Outside the breeding season, the Egyptian Goose in The Netherlands behaves as a resident species,[5,11] so the winter numbers reflect the population development of the Dutch birds. During the first years of its colonization, it was mainly observed in the vicinity of The Hague.[11,24] From 1976 onwards, the species

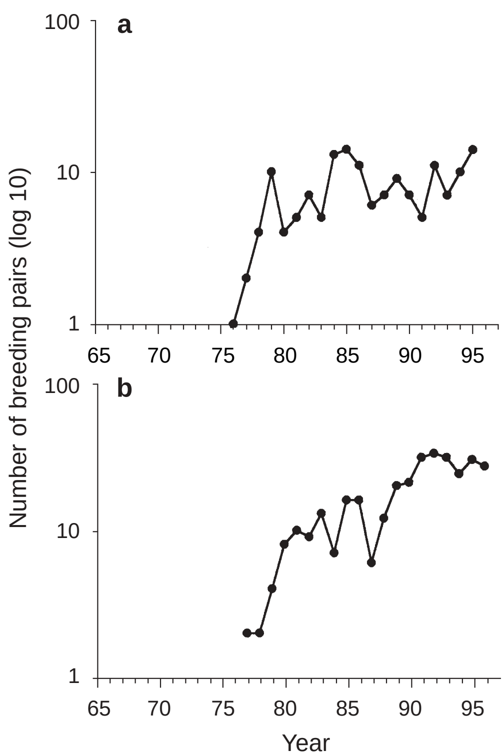

Figure 2. Changes in numbers of breeding pairs of Egyptian Goose in two survey areas in The Netherlands. (a) Berkheide; (b) Ooijpolder.

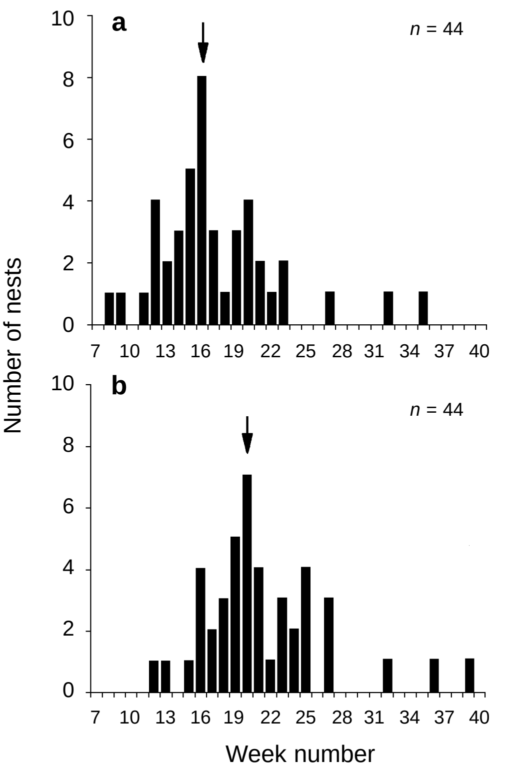

Figure 3. Timing of clutch completing (a) and hatching (b) in the census areas of Druten and Arnhem 1991–97. Data are summarized per week, week 20 is 14–20 May.

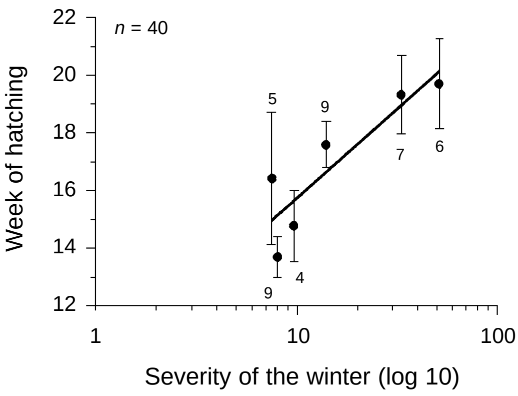

Figure 4. Relation between the timing of hatching and the severity of the preceeding winter. Data from the survey areas of Druten and Arnhem 1992–97. Numbers besides the data points show *n*, at the upper left the total *n* is shown. (regression line $y = 2.68 \ln(x) + 9.56$, $r = 0.887$, df = 5, $P < 0.01$).

occurred increasingly along the rivers IJssel, Rhine, Waal and Meuse, and the numbers counted increased exponentially (Fig. 2).

Breeding

Timing of incubation and hatching

In the survey areas of Druten and Arnhem, the first brood hatched young at the end of March (week 12) and the last in the last week (39) of September (Fig. 3). Most young hatched between the end of April and the beginning of July, with the median in week 20 (14–20 May). Hence, the first pair started breeding at the end of February and the last at the end of August (Fig. 3). Thus, the effective egg-laying period is 27 weeks. There was a positive relation between the mean time of hatching and the severity of the preceding winter (ANOVA, $F_{5,35} = 3.876$, $P < 0.01$) (Fig. 4). After the severe winters of 1995/96 and 1996/97, birds were 2–4 weeks later than in the other years.

Breeding success

There were no significant differences in overall breeding success between different dune or river survey areas. Therefore, the results were combined for each landscape type. The successful pairs in the coastal dunes raised a mean of 3.80 young, compared with 5.25 in the riverine areas (Table 1). The difference between areas was significant (*t*-test, $t = 3.57$, df = 97, $P < 0.001$), although there was no significant difference in the overall breeding success between the two areas (Mann–Whitney *U*-test, $z = -0.835$, ns). The main reason for this was the

Table 1. Breeding success of Egyptian Goose in two areas in The Netherlands 1977–96.

Area	n	*Young fledged all pairs*	*Successful pairs (%)*	*Young fledged per successful pair*
Coastal dunes	97	1.57 ± 2.40	41.2	3.80 ± 1.90
Riverine area	178	1.84 ± 2.74	35.0	5.25 ± 2.05

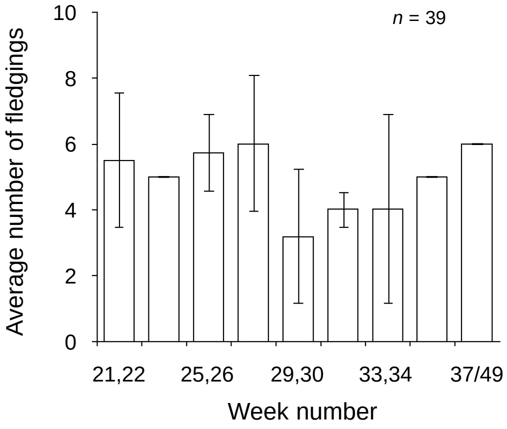

Figure 5. Average number of fledgings per successful pair in the course of the breeding season. Data from the survey areas Druten and Arnhem 1992–97.

high proportion of breeding pairs that failed to raise young in the dunes. There is no significant difference in the proportion of successful pairs ($\chi^2 = 0.76$, ns).

During the breeding season, the average number of young fledged did not change (ANOVA, $F_{2,99} = 1.843$, ns) (Fig. 5). Up to week 27/28, breeding success averaged between five and six fledged young, but fell significantly from an average of 6.0 fledging in week 27/28 to 3.1 in week 29/30 : least significant difference (LSD) test, $P < 0.05$. After that, breeding success increased; by week 36 the number of breeding Egyptian Geese was low, but those pairs were highly successful.

In the first year of breeding along the rivers (1977), two Egyptian Goose pairs each raised eight young. In later years, the proportion of successful pairs, as well as the overall number of fledglings produced decreased (Fig. 6). A negative correlation was found between these parameters and the number of pairs (percentage successful $r = –0.71$, $P < 0.05$, overall number of young fledged $r = –0.52$, $P < 0.05$). In the coastal dunes the same correlations were found, but neither was significant (percentage successful $R^2 = 0.38$, overall number of young fledged $R^2 = 0.35$).

During four of the 14 springs, the floodplains remained dry. In 1983 and 1987, the river flooded for over 25 days, mainly in May and June. In the other years, the number of days of inundation ranged between four and 17, mainly in April. In the Ooijpolder survey area,

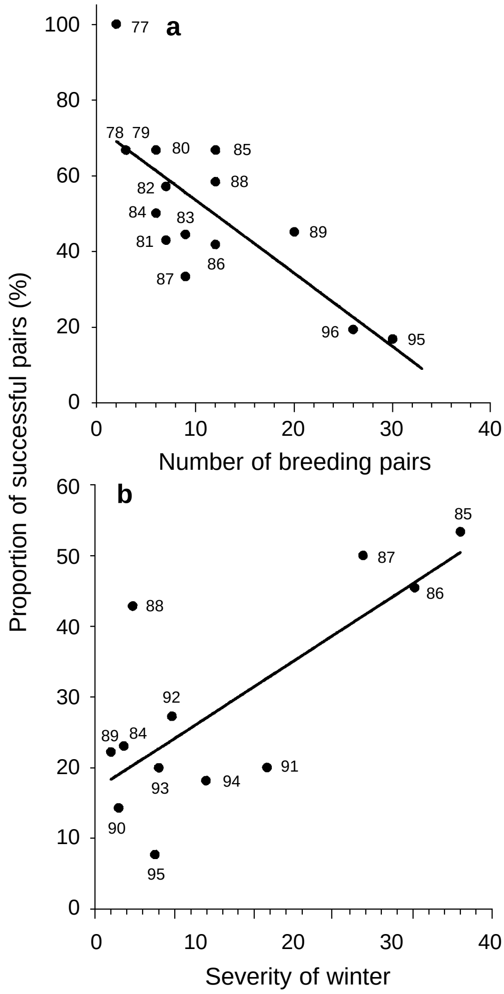

Figure 6. Relation between the overall breeding success of the Egyptian Goose and the number of breeding pairs in the survey area Ooijpolder (a, regression line $y = –1.937 + 72.87$, $r = 0.766$, df = 12, $P < 0.001$), and the severity of the winter in the survey area Berkheide (b, regression line $y = –0.731x$ 16.90, $r = 0.748$, df = 10, $P < 0.001$).

a negative correlation was found between the number of flooding days and the proportion of successful pairs ($r = –0.44$, $P < 0.05$), but not with the overall success ($r = –0.29$, $P > 0.05$).

Egyptian Goose pairs breeding in the coastal dunes produced, on average, significantly more young fledged after severe winters, than after moderate or mild winters (Fig. 6). The same relationship was found between the proportion of successful pairs and the severity of the winter ($R^2 = 0.61$, $P < 0.05$), but not for the

Table 2. Results of multiple regression on the breeding performance of the Egyptian Goose in the coastal dunes and along the rivers. The number of breeding pairs, the severity of the winter, and the number of inundation days (only along the rivers) are independent variables, whereas percentage successful pairs and overall number of fledglings were used as dependent variables. For the independent variables *beta* is given; *significant at $P < 0.05$.

	Statistics					*Independent variables*		
Area	R^2	*Adjusted* R^2	F	*df*	P	*Number of pairs*	*Winter severity*	*Inundation days*
Percentage successful pairs								
Dunes	0.564	0.439	4.523	2,7	0.055	–0.08	0.77*	–
Rivers	0.663	0.551	5.911	3,9	0.016	–0.81*	–0.16	–0.34
Overall success								
Dunes	0.767	0.690	9.897	2,6	0.013	–0.13	0.86*	–
Rivers	0.543	0.314	2.373	3,6	0.169	–0.65*	–0.18	–0.40

average number of fledged young from successful pairs ($R^2 = 0.05$, ns). For Egyptian Geese breeding along the rivers, similar relationships were found, but none of them was significant (overall success $R^2 = 0.435$, percentage successful $R^2 = 0.283$, and successful pairs $R^2 = 0.05$, all ns).

In both areas, a positive correlation was found between the success of Egyptian Geese and the severity of the winter. Along the rivers, a negative correlation was found between success and the number of breeding pairs as well as the number of flooding days in the breeding season. These findings were put into a series of linear models (Table 2). These analyses showed that, in the coastal dunes, the winter severity was the most important factor in explaining differences in breeding success, while along the rivers the most important factor was the number of breeding pairs, followed by winter severity and inundation respectively. Furthermore, in the dune area the model that used the proportion of successful pairs was the most explicative, whereas in the riverine habitat the model that used the proportion of successful pairs was most explicative.

Survival of young

The pairs that were followed in detail had on average 5.5 young in the first week after hatching (Fig. 7). Four weeks later just 4.6 young were left. In the last weeks before fledging, pairs were accompanied by on average 4.4 young. This means a decline in the number of young of 20.0% during the dependent period. Of the 34 pairs under study, two pairs finally fledged no young (5.9%). These had hatched two and three young. The overall trend in the decrease in young was significant (MANOVA, $F_{1,99} = 401.01$, $P < 0.001$). The difference between the first and second periods is not significant (LSD test, ns), mainly because of the wide range of 0–10 young per pair. The first and third periods differed significantly (LSD test, $P < 0.05$).

Non-breeding

Outside the breeding season, flocks of Egyptian Geese gather in the vicinity of their breeding

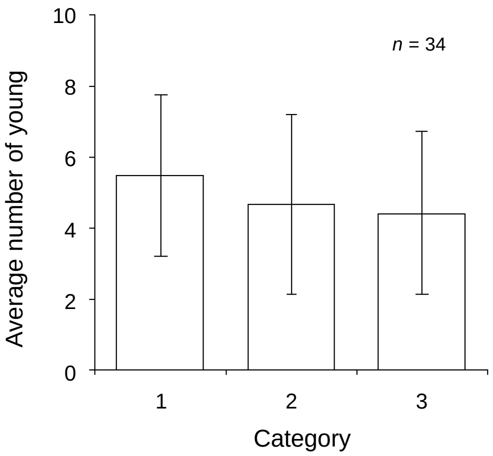

Figure 7. Average number of young in three age-classes (1–2 weeks, 4–5 weeks and 8–10 weeks old) in the period before fledging.

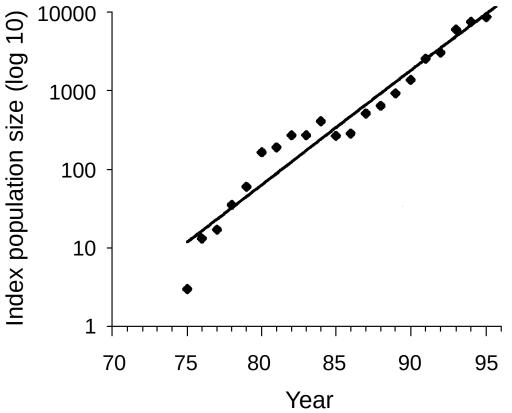

Figure 8. Seasonal (September–April) total of Egyptian Goose along the rivers IJssel, Rhine, Waal and Meuse in the Netherlands 1969–95 (75 = 1975/76) (regression line $y = 0.01\ e^{0,3335x}$, $r = 0.970$, df = 20, $P < 0.001$).

sites.[5,6] Along the rivers in The Netherlands, the population of Egyptian Geese has increased since 1976 (Fig. 8). The highest numbers were counted in December each year (Fig. 9). Thereafter, in the subsequent months the number slowly decreased. During severe winters, the fall in numbers between December and January/February was about 60%, whereas the fall during mild and moderate winters was less. There was a negative correlation between winter severity and the ratio of the number counted in spring relative to that in autumn ($r = 0.589$, df = 17, $P < 0.05$). No correlation could be found between the number of inundation days of the river floodplains and the ratio of the number in spring relative to autumn (number of days in spring $r = 0.032$, number of days in autumn $r = 0.063$, both df = 17, ns).

The previous section showed that winter severity has a negative impact on the population size, so there should be a relation between this and the population increase in subsequent years. The increase in the autumn numbers of Geese in subsequent years shows no correlation with the severity of the winter after the first autumn ($r = -0.340$, df = 15, ns), implying that the population size in subsequent autumns is not negatively influenced by the preceding winter. The increase in spring numbers in subsequent years is positively correlated with the severity of the preceding winter ($r = 0.556$,

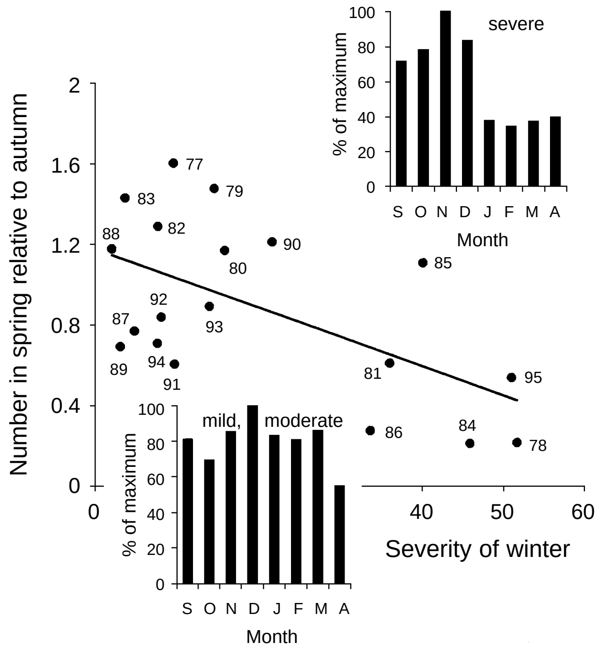

Figure 9. Relation between the decrease in numbers during winter and the severity of the winter. The decrease is expressed as the total number in October–December relative to those in January–March (78 = 1978/79), (regression line $y = -0.015x + 1.174$, $r = 0.589$, df = 19, $P < 0.001$).

df = 15, $P < 0.05$). Thus, after a severe winter, which mainly affects conditions in January and February, the numbers can increase quite dramatically after the next winter. If the first severe winter is followed by a second, as in 1985/86, the numbers decline further.

DISCUSSION

Data limitations

Most data for this study were collected during fieldwork for the Dutch Common Breeding Bird Census. This means that observers' attention was not solely focused on the Egyptian Goose. For studies on breeding biology, a visit frequency of every 10–14 days is low. The timing and progress of the breeding cycle was derived from an estimate of the age of young. Size and plumage development give good indications of the age of the young, but mistakes of half a week can be made. For this reason, summarizing data per week seems to be appropriate. Once a pair with young was found, they were easy to relocate and to follow during further visits. Despite this inaccuracy in the data, the overall results are clear enough to give some confidence.

Breeding parameters

Timing of breeding

The breeding season for the Egyptian Goose in The Netherlands starts at the end of February and can last until the end of November. The data for first egg-laying can vary by more than six months (Fig. 1), as shown by another Dutch study.[25] In tropical Africa, the species can breed all year round, although most breed just before the rainy season starts, to coincide with the availability of green pastures.[26] In regions with one wet period, there is generally one peak in breeding, and in regions with two periods, two peaks.[1] In Europe, most geese and waterfowl species have a relatively short breeding period, which lasts on average 2–3 months between the earliest and latest pairs.[19] In the closely related Shelduck *Tadorna tadorna,* this period is about the same.[19] The Egyptian Goose in Europe, therefore probably behaves as in Africa, breeding when conditions are favourable. Outside of winter, it takes any opportunity to breed, with apparent success.

There was a positive correlation between the mean time of hatching and the severity of the preceding winter (Fig. 4). This was found most strikingly after the severe winters of 1995/96 and 1996/97, when birds were 2–4 weeks later than in the other years. On the other hand, in 1995 a great deviation from the average was found. This was due to the prolonged and high flooding of the river floodplains in winter and spring 1995. Birds breeding on sites not directly influenced by the water levels in the river, were found breeding early, as could be expected by the relatively high winter temperatures. The other pairs had to wait until feeding grounds and breeding sites dried out during March and April.

Breeding results

To assess the relative success of the Egyptian Goose in Europe, we need to look at the breeding success relative to Africa. Eltringham[26] studied the reproduction of the Egyptian Goose in Uganda. Successful pairs produced on average 6.5 young. Approximately 10% of the pairs breed more than once a year.[2] Thus, the average number of young per year for successful pairs is 7.3. The proportion of successful pairs in his study was 47%. Based on the presence of non-breeding adults, or adults with failed nests,[2] the real nest success was lower in the same area. Juvenile survival in the first two months was about 60%. On average, the number fledged was therefore less than 2.0, compared with an average of 2.0 in The Netherlands. Thus, survival in the first two months of life in the Egyptian Goose is lower in Uganda. The lower survival rate in this part of Africa can be attributed to the high number of (potential) predators present there,[2] which are largely lacking in western Europe. Here there are few predators, as far as we know.

In England, breeding success seems to be lower than in The Netherlands. During their study, Sutherland & Allport[6] found an average of about 1.0 fledged young per pair, whereas in The Netherlands birds fledged nearly 2.0 young (Table 2). This can make the difference between the rapid growing population in The Netherlands and a more or less stable population in Britain. In Britain, as well as The Netherlands, most breeding attempts are found in sites with short grass for chicks to graze, open water for protection of the young and a suitable nest-site such as islands, old trees with holes or epicormic shoots.[5,6] The reasons for the differences in breeding success could lay in climatological differences between the areas, differing predation rates or genetic differences between the two feral populations.

Breeding success in the field was estimated for two different habitats (Table 1). Breeding success differed significantly between them. There are two possible explanations. They could differ in habitat quality and predation pressure. In the dunes of the western Netherlands good feeding opportunities are limited, which is not the case in the river areas. However, it is unknown whether habitats differ in clutch size. The density of Foxes *Vulpes vulpes* in the dunes seems to be higher than in the river areas (Verstrael, Bekhuis, pers. comm.). Yet, in both landscapes Egyptian Geese breed in trees and old nests of other birds. A second explanation is that, in the dune area, only environmental factors caused differences between years, because data were collected only after 1984, when the increase in breeding numbers had stopped. Along the rivers, the average was calculated for the colonization period, which lasted until 1990. In the Ooijpolder, for example, colonization seems to have stopped after 1992. During 1995 and 1996, only 20% of the 26 pairs successfully raised young. Fieldwork over the next few years should reveal a great deal more about the Dutch Egyptian Geese.

Factors affecting the breeding population

In Ooijpolder, a strong correlation was found between breeding success and the number of breeding pairs. After the first successful breeding attempts in this area, the breeding success decreased. In Berkheide, a strong correlation was found between breeding success and the severity of the winter. Data in the latter area were collected after the Egyptian Goose had colonized this area and the population became more or less stable. In both areas, the decrease in overall breeding success was caused by a lowering in the proportion of successful pairs, and not in the average number of fledged young of the successful pairs. Therefore, overall breeding success in the Egyptian Goose seems to be influenced by density-dependent factors, soon after the colonization starts. After colonization has reached its maximum, environmental factors become more important.

The Egyptian Goose is highly territorial, mostly against congeners and less so towards other species.[1,19] Defending a territory may be an energetically costly business. One can conceive that early in colonization, with just a few neighbours, pairs can put most of their energy into reproductive effort. It is also plausible that the first colonizing pairs are breeding in the best habitats. Later during colonization, pairs have to spend more time and energy in defending their territory, while vacant breeding sites are likely to be of lesser quality. Both factors could be responsible for a decline in breeding success during colonization. In comparison, the increase in the numbers of breeding Barnacle Geese in the Baltic area was accompanied by a decrease in the proportion of successful breeding attempts.[27]

The severity of the winter influences different stages in the annual cycle of the Egyptian Goose in The Netherlands. In spring, a severe winter causes a delay in the onset of incubation. At the later time that young hatch, the weather is generally better. Differences in overall success between years are mainly caused by differences in the proportion of successful pairs. Analysis of counts outside the breeding season have revealed a relatively high mortality during severe winters. After such winters, in most cases, the Dutch breeding population stabilized or even decreased. In the case of a decline, following a severe winter, the density in breeding areas was lower than in the year before, so giving birds the opportunity to invest more energy in their reproductive effort instead of defending their territories.

The Egyptian Goose has colonized The Netherlands successfully. On a local scale, soon after the colonization started, density-dependent factors appear to have started to operate. The principal effect is that the number of pairs, which successfully raise young, declined. However, the number of birds in the population was negatively affected by severe winters. Birds can compensate for the losses during a hard winter by a prolonged breeding season and a delay in the onset of the breeding period after a severe winter.

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REFERENCES

1. Brown, L., Urban, K. & Newman, P. (1982) *Birds of Africa,* Vol. 1. Academic Press, New York.
2. Eltringham, S.K. (1974) Fluctuations in the numbers of wildfowl on an equatorial hippo wallow. *Wildfowl,* **24,** 81–87.
3. Curry-Lindahl, K. (1981) *Bird Migration in Africa,* Vol. 1. Academic Press, London.
4. Oatly, T.B. & Prys-Jones, R.P. (1985) A comparative analysis of movements of southern African waterfowl (*Anatidae*), based on ringing recoveries. *S. Afr. J. Wildl. Res.* **16,** 1–6.
5. Lensink, R. (1996) De opkomst van exoten in de Nederlandse avifauna, verleden, heden en toekomst. *Limosa* **69,** 103–130. (in Dutch with English summary)
6. Sutherland, W.J. & Allport, G. (1991) The distribution and ecology of naturalized Egyptian Geese *Alopochen aegyptiacus* in Britain. *Bird Study,* **38,** 128–134.
7. Kear, J. (1989) *Man and Wildfowl.* Poyser, Calton.
8. Sharrock, T. (ed.) (1976). *The Atlas of Breeding Birds in Britain and Ireland.* Poyser, Calton.
9. Delany, S. (1993) Introduced and escaped geese in Britain in summer 1991. *Br. Birds,* **86,** 591–600.
10. Prater, T. (1993) Egyptian Geese. In *The New Atlas of Breeding Birds in Britain and Ireland: 1988–91* (eds D.W. Gibbons, J.B. Reid, & R.A. Chapman). Poyser, Calton.
11. Teixeira, R.M. (ed.) (1979) *Atlas van de Nederlandse Broedvogels.* Natuurmonumenten, 's Graveland. (in Dutch)
12. Lensink , R. (1998) Temporal and spatial expansion of the Egyptian Goose *Alopochen aegyptiacus* in The Netherlands, 1967–94. *J. Biogeogr.* **25,** 251–263.
13. Devillers, P. (1988) *Atlas van de Belgische broedvogels.* Koninklijk Belgisch Instituut voor Natuurwetenschappen, Brussels. (in Dutch)
14. Anselin, A. & Devos, K. (1992) *Populatieschattingen van Broedvogels in Vlaanderen 1989–91.* Report, Valvico, Gent. (in Dutch)
15. Boyd, H. (1964) Wildfowl and other water-birds found dead in England and Wales in January-March 1963. *Wildfowl,* **15,** 20–22.
16. Meininger, P.L., Blomert, A.M. & Marteijn, E.C.L. (1991) Sterfte onder watervogels in het deltagebied, ZW-Nederland, tijdens de drie strenge winters van 1985, 1986 en 1987. *Limosa,* **64,** 89–102. (in Dutch with English summary)
17. van Dijk, A.J. (1985) *Handleiding Broedvogel Monitoring Project.* SOVON, Arnhem.
18. Bibby, C.J., Burgess, N.D. & Hill, D.A. (1992) *Bird Census Techniques.* Academic Press, New York.
19. Cramp, S. & Simmons, K.E.L. (1977) *Handbook of the Birds of the Western Palearctic,* Vol. 1. Oxford University Press, Oxford.
20. Siegfried, W.R. (1967) Trapping and ringing of Egyptian Geese and African Shelduck at Vogelvlei, Cape. *Ostrich,* **38,** 173–178.
21. IJnsen, F. (1991) Karaktergetallen van de winters sinds 1707. *Zenith,* **18,** 69–73. (in Dutch)
22. Van Ommering, G. & Verstrael, T.J. (1987) *Vogels van Berkheide.* Stichting Duinbehoud, Leiden. (in Dutch)
23. Erhart, F. & Bekhuis J. (1996) *Broedvogels van de Gelderse Poort 1989–1994.* VWG Arnhem e.o./VWG Rijk van Nijmegen e.o./NABU Naturschutzstation Kranenburg, Arnhem. (in Dutch)
24. SOVON (eds) (1987) *Atlas van de Nederlandse Vogels.* SOVON, Arnhem. (in Dutch with English summary)
25. Venema, P. (1990) De Nijlgans *Alopochen aegyptiacus* in Drenthe 1980–91. *Drentse Vogels,* **5,** 3–11. (in Dutch with English summary)
26. Eltringham, S.K. (1973) The survival of broods of the Egyptian Goose in Uganda. *Wildfowl,* **25,** 41–48.
27. Larsson, K. & Forslund, P. (1994) Population dynamics of the Barnacle Goose *Branta leucopsis* in the Baltic area: density-dependent effects on reproduction. *J. Anim. Ecol.,* **63,** 954–962.

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