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Temporal and spatial expansion of the Egyptian goose *Alopochen aegyptiacus* in The Netherlands, 1967–94

ROB LENSINK *Working Group on Animal Ecology, Department of Ecology, Catholic University of Nijmegen, Toernooiveld 1, PO Box 9010, 6500 GL Nijmegen, The Netherlands*

Abstract. In this paper, the temporal and spatial expansion of the Egyptian goose in the Netherlands are described and analysed. The species bred near The Hague for the first time in 1967. In 1983 a second settlement developed in Drenthe. Both settlements expanded. Together, they contained about 1340 breeding pairs in 1994. For both settlements a linear relationship exists between the square root of the area occupied and time. In both cases, population growth is exponential. The bird behaves as a resident species. Thus, in winter numbers in The Netherlands also increase exponentially. The Egyptian goose seems to be sensitive to severe winters, which cause a high mortality. The observed velocity of range expansion is compared with the velocity as calculated with the expansion model of Van den Bosch *et al*. (1990). The observed velocity was about 3.0 km per year, which is about 20% lower than expected, but not significantly different. Population growth was estimated using a projection matrix. In the first 10 years after its settlement near The Hague, the actual population growth was larger than the calculated growth. There is evidence for good breeding success during the first years due to mild winters between 1972 and 1978. In the second settlement, Drenthe, the same rapid population growth occurred. Here, a low but regular influx of birds from a nearby city park was probably the main factor. In the near future, further temporal and spatial expansion can be expected, in the direction of Germany and Denmark in the east and Belgium and France in the south. Towards the east the severity of the winters might limit further range expansion, possibly coinciding with the 0° isotherm in January.

Key words. Egyptian goose, range expansion, release, population growth, dispersal, life history parameters, feral population.

INTRODUCTION

In this paper, the successful colonization of the Netherlands by the Egyptian goose *Alopochen aegyptiacus* will be described and analysed. This species is native in Africa; its breeding grounds are mainly south of the Sahara and in the upper Nile Valley (Brown, Urban & Newman, 1982; Goodmann & Meininger, 1989). In the seventeenth century the species was introduced into Great Britain, mainly as ornamental waterfowl (Kear, 1990). Since then a feral population has established (Sharrock, 1976; Lever, 1987; Gibbons, Reid & Chapman, 1993). On the European mainland the species was also introduced. Here, birds were held in captivity and in city parks. Since 1967, a feral population has developed in The Netherlands (Teixeira, 1979; Lever, 1987).

The introduction and subsequent expansion of plant and animal species outside their native area has long caught the interest of ecologists (Elton, 1958; Williamson & Brown, 1986, and many others). Among birds, the successful colonization of the New World by the starling *Sturnus vulgaris*, the house sparrow *Passer domesticus* and the cattle egret *Bubulcus ibis*, and of Europe by the collared dove *Streptopelia decaocto* are classic examples (Hengeveld, 1987; Hengeveld & Van den Bosch, 1991; Van den Bosch, Hengeveld & Metz, 1992). The rate of increase and the velocity of range expansion are important characteristics of a successful colonization (Mooney & Drake, 1986; Groves 1986; Kornberg & Williamson, 1987; Hengeveld, 1987, 1989; Hengeveld & Van den Bosch, 1991, and many others).

Much effort has been put into formulating mathematical models that describe the velocity of range expansion, based on first principles such as reproduction, survival and dispersal. The most popular model was formulated by Skellam (1951). He assumed that (1) all individuals are identical as to reproduction and survival, (2) all individuals move at random through space, and (3) there is an exponential population growth. In birds, it is known that the first two assumptions are unrealistic. Reproduction and survival do depend on age and after their juvenile stage, many individuals settle more or less permanently in one breeding area. The model formulated by Van den Bosch, Metz & Diekmann (1990) seems to be more realistic with regard to both points (Hengeveld, 1994). This model is based on reproduction, survival and dispersal at the level of the individual bird. Furthermore, Van den Bosch *et al*. (1992) have claimed that this model in this case gives better predictions than the Fisher–Skellam model.

Present address and correspondence: Hogestraat 17, NL, 6651-BG Druten, The Netherlands.

Leslie (1945) successfully introduced projection matrices in the modelling of populations. Those matrices are based on reproduction and survival at the level of individuals. They give information on the rate of density independent population growth and the (relative) sensitivity of the growth rate by a change in one or more elements of the matrix. Use of these matrices gives a realistic view on the behaviour of a (bird) population (Van Groenendael, De Kroon & Caswell, 1988; Caswell, 1989; Lebreton & Colbert, 1991).

I will compare the observed velocity of range expansion and the values calculated with the expansion model, to show how important the dispersal ability of the Egyptian goose is for successful colonization. Furthermore, comparison is made between the observed rates of population growth with the values calculated with a matrix model, to evaluate whether the first breeding pairs near The Hague were a sufficient propagule to cause the increase in breeding numbers up to 1994.

For calculating both models, life–history parameters are applied as measured in the field. The observed values of life history parameters reached in The Netherlands are evaluated in light of those obtained in Africa. This comparison shows the ecological possibilities of this species in north western Europe; collating all the known information so far will contribute to a further understanding and assessment of the colonization of western Europe by the Egyptian goose.

METHODS

Census of breeding Egyptian geese

The data used in this paper on the rates of population growth and range expansion of the Egyptian goose have been extensively accounted for in Lensink (1996). Here, only the different sources and methods are summarized.

Teixeira (1979) documented the start of the development of the feral population (1967–1977). For the period 1978–83, much information on range expansion was collected in connection with the year–round atlas project in The Netherlands (SOVON, 1987). To compile the distribution and numbers for 1984–94, in 1994 an extensive questionnaire was distributed among hundreds of observers in The Netherlands. Databases on the national breeding bird census were also used (SOVON/CBS). Thereafter, all sources of information were screened to exclude double observations. All data on the breeding of Egyptian goose in different areas concerned probable and confirmed breeding. 'Probable' breeding means that in the breeding season a territorial pair (courtship, display, agitation) was observed. 'Confirmed' breeding means that distraction–display was seen or adults with downy young, or a nest with eggs or chicks was found (see further Sharrock, 1976).

Data on the breeding success of the Egyptian goose were collected at six places in the Netherlands, i.e. in three dune areas north of The Hague in the west, and in three river areas in the eastern part of The Netherlands (Fig. 1). Most of the data were collected at intervals of 10–14 days from March to July during the fieldwork done for the national breeding bird census by observers visiting census areas. From these data, a number of territorial pairs (= breeding) can be derived (Hustings *et al*., 1984; Bibby, Burgess & Hill, 1992, Van Dijk, 1993). At each visit, the number of juvenile birds was recorded. Nesting success is expressed as the proportion of pairs with young on open water (see Eltringham, 1975). The real nesting success may be somewhat higher, as on average the young are 1 week old at the time of first sighting. From these consecutive observations of the number of young, the rate of survival in the pre–fledgling period can be calculated. At the next stage, they become fledged (Eltringham, 1975; Cramp & Simmons, 1977).

Analysing time series of distribution maps

From a time series of successive distribution maps the velocity of range expansion can be calculated, the so-called 'area method' (Van den Bosch *et al*., 1990; see also Williamson & Brown, 1986; Andow *et al*., 1990). This method describes the advance of an invading species as a travelling wave with constant speed, expressed by the linear relationship between the square root of the area occupied and time (Skellam, 1951). In mathematical terms, the area covered can be written as:

$$A_t = \pi(r_t)^2 = \pi(O_m + C_{(t-m)})^2$$

where r_t is the radius r at time t, C the velocity of range expansion and O_m a correction factor O for the initial period of population build up with length m. Thus the square root of the area is the best linearization of the time course of the spread of an invasion. The velocity of range expansion, C, can be calculated from the slope of this line, where the initial period should be excluded. Furthermore, a correction has to be made for the intersection of the whole circle that is under consideration (Van den Bosch *et al*., 1990). In this study, the number of squares (5×5 km) within the continuous distribution range was taken as a measure of the area covered by the Egyptian goose. Foci ahead of the travelling wave of expansion were excluded.

Census of Egyptian geese during the winter

Since 1969 in The Netherlands along the Rivers Rhine, Waal, IJssel and Meuse, regular and standardized waterfowl counts have been conducted from September to April (Hustings *et al*., 1984; Bibby *et al*., 1992). Counts are usually made around the 15th of each month. All waterfowl present are recorded on adjacent transects along the rivers. The data from these counts are used for estimating population size and development within and between winter seasons (Lensink, 1996).

Dispersal of new breeding pairs

The distance between the birth place and the breeding place of a bird is defined as the dispersal distance. For its African breeding range, data on the dispersal distance are lacking (T. Oatley (SAFRING, South Africa), pers. comm.). The best method for estimating this distance would be to ring juvenile birds on their nest and record them in later years

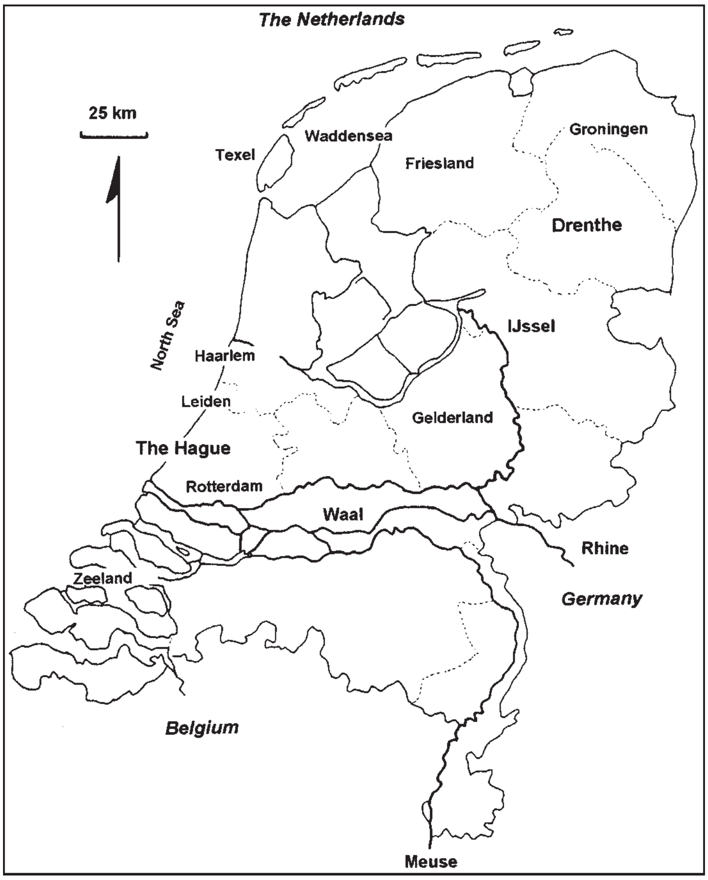

FIG. 1. Map of The Netherlands with the locations mentioned in the text.

at their actual breeding site. As this was not possible, an analysis was made of distribution maps of breeding Egyptian goose along the rivers Rhine, Waal and IJssel in the eastern part of the Netherlands. For this, maps of 1977, 1983, 1989 and 1994 were prepared, each containing the exact location of the nests/territories in these years (J. Bekhuis, pers. comm., V.W.G. Arnhem, pers. comm., Lensink, 1993). The minimum distance between old and new sites on two successive maps was used as the dispersal distance. This is certainly an underestimation.

Model of range expansion

The model of the range expansion used here is based on three life–history characteristics at the level of the individual bird. The model takes only the *female* part of the population into account. Using these characteristics, the velocity of range expansion C can be calculated (Van den Bosch *et al.*, 1990, 1992).

The first characteristic is the age–specific survivorship, $L(a)$. It is defined as the probability that an individual is still alive at time a after its birth. The second is the age–specific fertility, $m(a)$. It is defined as the rate of reproductive offspring at age a. These two characteristics describe the number of young produced and the time of reproduction. It is assumed that Egyptian geese disperse as juveniles after which they settle definitively at one breeding site, as is known for many other bird species (see Cramp & Simmons, 1977). The third parameter is the dispersal density D, defined as the probability per unit area that an individual hatched at place z settles at place x ($D(x_1,x_2,z_1,z_2)$). This probability is assumed to be a function of the distance between the places of hatching and settlement only; the assumption implies that there is no preference in dispersal direction.

Van den Bosch *et al.* (1990, 1992) have shown that by using these three characteristics, the velocity C of the spatial expansion of the population can be approximated by:

$$C = (\sigma/\mu)^* \sqrt{(2 \ln R_o)}.$$

The net reproduction rate R_o, representing the total number of offspring produced during the whole life of an individual, is written as:

$$R_o = \int_0^\infty L(a)\, m(a)\, da.$$

The mean age of egg laying μ is written as:

$$\mu = (I/R_o) \int_0^\infty a\, L(a)\, m(a)\, da.$$

Calculations of the parameters R_o and μ were done from life–tables. Calculations of R_o were done up to the age–class in which less than 1% of the initial number (100%) was still alive. The variance σ^2 of the marginal density of the sites where the individuals settle relative to their birth place is written as:

$$\mu^2 = \int_{-\infty}^{\infty}\int_{0}^{\infty} x_i^2\, D(x_1,x_2)dx_1,dx_2.$$

The standard deviation σ of the dispersal distances is a measure of how far from its own place of birth an average individual will give birth to his own offspring. It can be calculated from the dispersal distances found in the field.

Model of population growth

The growth of a population can be described in the form of a Leslie matrix (Leslie, 1945; Van Groenendael *et al.*. 1988; Caswell, 1989). Only the *female* part of population is considered in the matrix, assuming a 1:1 sex ratio and equal survival rates of both sexes, as is common practice in population growth models of sexually reproducing organisms (Charlesworth, 1980). For the Egyptian goose, the sex ratio is about 1:1, as was observed in a stable population in South Africa (Siegfried, 1967). Fledged females of up to 1 year old are designated as *1 Y*, up to 2 years as *2 Y*, and older females as *>2 Y*. Since Egyptian geese breed for the first time when they are 2 years old, they have survived two winters before starting their first brood (Del Hoyo, Elliot & Sargatal, 1993). Age-specific survival (*s*) and fecundity (*f*) were assigned to the various age groups. Fecundity was calculated as the product of (1) the proportion of breeding attempts that were successful, and (2) the mean number of fledged females per successful breeding attempt. Since *1 Y*–individuals and *2 Y*–individuals do not breed, *f* is zero for these age groups. The survival of 1Y, 2Y and >2Y females was presumed (see further). The matrix thus becomes:

$$M(t) = \begin{bmatrix} 0 & 0 & f_3 \\ s_1 & 0 & 0 \\ 0 & s_2 & s_3 \end{bmatrix}$$

The time interval for calculations with the matrix is 1 year. The number of females at year t is:

$$N(t) = \begin{bmatrix} N_1(t) \\ N_2(t) \\ N_3(t) \end{bmatrix}$$

where $N_I(t)$ stands for the number of *1 Y* females, etc. The number of females at year $t+1$ is

$$N(t+1) = M(t)*N(t)$$

Application of life–history parameters

To apply the models of range expansion and population growth, breeding success was implemented as measured in the field. Breeding success is given as an average of all age classes. In reality, breeding success is age dependent, as shown for many bird species (Charlesworth, 1980) such as swans and geese (Newton, 1989; Forslund & Larsson, 1992). For the purpose of this study the use of the average number of fledglings was good enough, because it was assumed that all age classes are represented in the average, pro rata to their occurrence in the field.

The dispersal distances, as estimated from a time series of maps (see above), were put into the model of range expansion. Since in the distibution of dispersal distances long-distance dispersal is underestimated, an assumed distribution (Table 3) was also used.

The survival rate of the Egyptian goose is not known. For this reason, the models are calculated for a range of survival rates, for *1 Y* birds as well as *>1 Y* birds. The range varies between 0.6 and 0.7 for young and 0.6 and 0.9 for adults, covering the full range of survival rates of the larger duck species and smaller goose species (Cramp & Simmons, 1977; Ebbinge, 1993).

Weather

In The Netherlands and other countries in north western Europe, the severity of the winter is an important factor for the survival of resident or wintering waterfowl (Boyd, 1964; Meininger, Blomert & Marteijn, 1991, and others). For this reason the relationship between winter severity and rate of increase of the number of Egyptian geese was examined. The Royal Dutch Meteorological Institute (KNMI) supplied data on the severity of winters. The severity index V was calculated as (IJnsen, 1991).

$$V = v^2/363 + 2*y/3 + 10*z/9,$$

where v is the number of frosty days (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 with V>25 are considered severe (IJnsen, 1991; KNMI).

RESULTS

Colonization of The Netherlands

The first successful breeding attempt of the Egyptian goose took place near The Hague in 1967. These birds had probably escaped from a park in this city (Teixeira, 1979; Lever, 1987). A feral population developed in these surroundings during the following years. From 1971 onwards, the species spread over the vincinity of The Hague, as well as in the direction of Rotterdam (Fig. 2). In 1976 it settled near Haarlem, 50 km north of The Hague, and in 1978 in extensive peatland marshes 40–50 km east of The Hague. These breeding sites were new foci far ahead of the main travelling wave, and showed the ability for long–distance dispersal of the Egyptian goose. In 1977, a pair bred successfully near the River Rhine close to the German border. These birds presumably originated from the western part of The Netherlands, and formed the beginning of a successful colonization of the area along the Rivers Rhine, Waal, IJssel, and Meuse in the eastern part

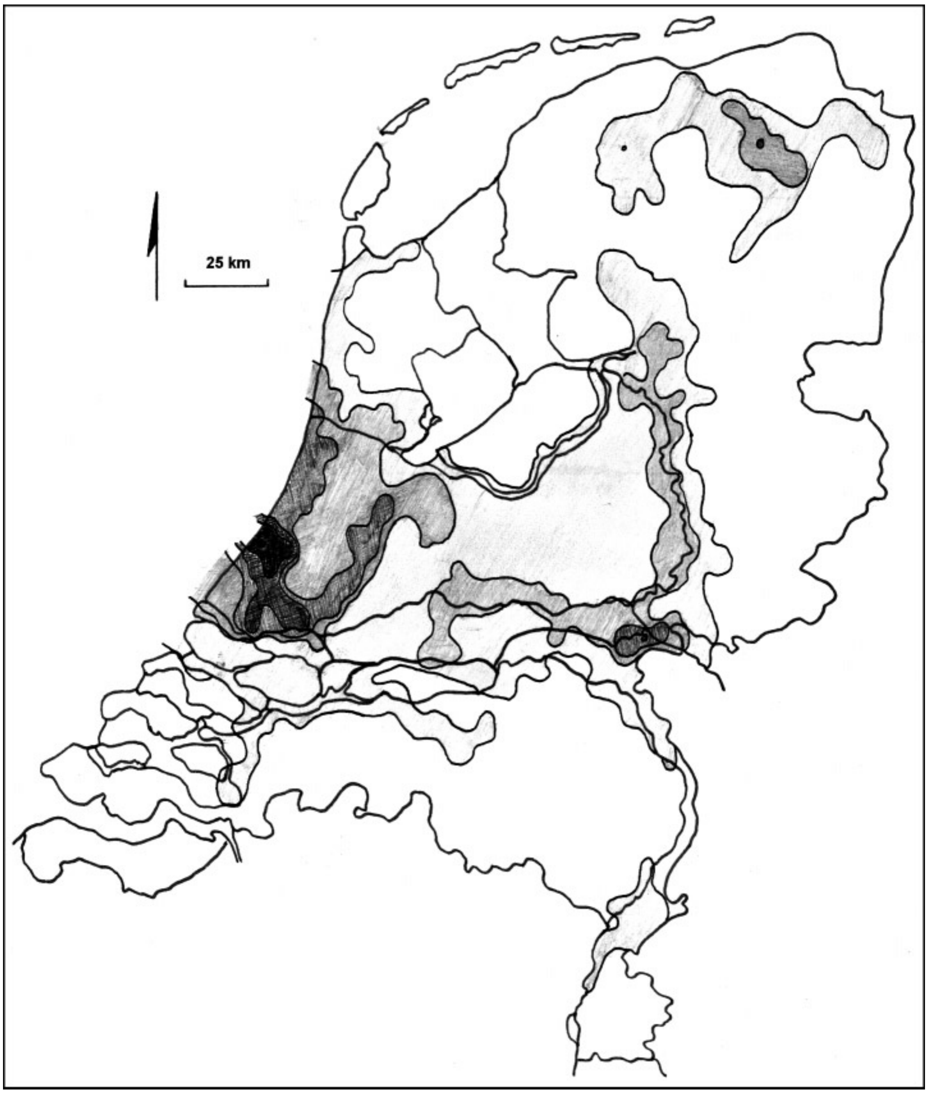

FIG. 2. Distribution range of the Egyptian goose in The Netherlands in 1972, 1977, 1983, 1989 and 1994 (A), distribution map 1977 (B), distribution map 1994 (C) (after Lensink, 1996).

of The Netherlands. In the 1980s it occupied large areas in the central parts of the country, and since 1983 it has been breeding in large peatland marshes near the mouth of the River IJssel. Up to 1994, the Egyptian goose spread further south along the River Meuse, and settled in the province of Zeeland in the south west of the country. In 1993 it occupied the most western island (Texel) in the Waddensea area.

In 1981 or 1982, birds from a city park in Groningen in the north east of The Netherlands settled in a peatland marsh in the adjacent province of Drenthe. These birds were the first propagules of the colonization of the three provinces in the north east of the Netherlands (Fig. 2). I assume that the birds in the province of Friesland originate from the Drenthe settlement. In Friesland the first pairs were observed at the time that the population in Drenthe increased rapidly, and the number of pairs in the mouth of the IJssel was still very low (1986–87). Two years later the latter pairs expanded further northward.

In 1991, the first breeding attempt was made across the German border along the River Rhine. In 1993 breeding was also observed along the northern part of the River Eems in Germany, 20 km east of the border with The Netherlands. In 1994 there was a total of about five to eight breeding pairs in Germany, all near the Dutch border. In this year the Egyptian goose, originating from only two Dutch settlements, remained mainly within the borders of the Netherlands.

The area occupied by the Egyptian goose increased in subsequent years (Fig. 3). After settling near The Hague, during the first 10 years the area occupied increased more slowly compared to the following 15 years (test on slope, $t = 3.506$, d.f. $= 6$, $P < 0.05$). For the whole period, a velocity of range expansion of 3.0 km per year has been calculated (Table 1). For 1967–77, this value is 1.16 km per year and for 1977–94 4.59 km per year. In the north of the Netherlands, the velocity of range expansion in 1983–94 was 2.00 km per year, not faster compared to the first 11

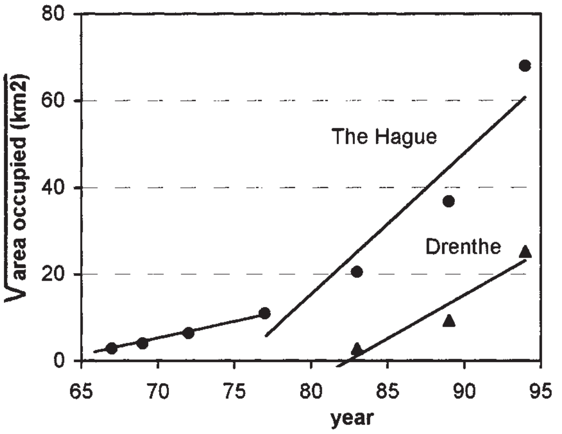

FIG. 3. Square root of the area occupied (km) against time (years) for the settlements of The Hague and Drenthe separately. Regression lines are fitted by means of least squares (see Table 3 for statistics). The period 1967–77 is the initial phase of expansion and the period 1977–94 the period of constant spread.

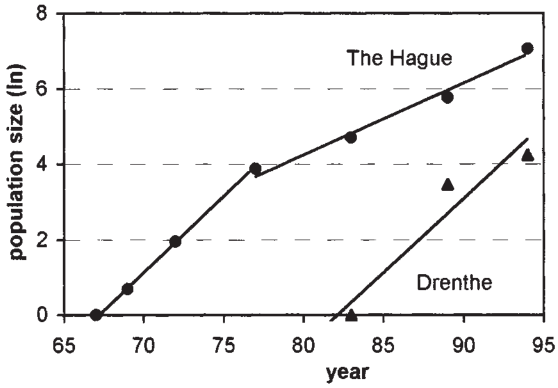

FIG. 4. The number (ln scale) of breeding Egyptian goose in the Netherlands in 1969–94. Regression lines are fitted by means of least squares (The Hague 1967–77, $r=0.999$, d.f.$=3$, $P<0.001$, The Hague 1977–94, $r=0.990$, d.f.$=3$, $P<0.001$, Drenthe 1983–94, $r=0.956$, d.f.$=2$, $P<0.05$).

years of the settlement near The Hague ($t=1.47$, d.f.$=5$, $P>0.10$). The settlement near The Hague started near the North Sea. Here, expansion was only possible in the direction of a half circle instead of a whole circle; this explains why the velocity, following from the regression line in Fig. 3, is multiplied by $\sqrt{2}$ (Van den Bosch *et al.*, 1992). The settlement in the province of Drenthe could expand in all directions, not needing this correction.

Biotope

Breeding Egyptian goose are found in four main biotope types. In the dune area along the North Sea, they breed along (artificial) infiltration lakes and canals for drinking water supply. Along the rivers they are found breeding in claypits, oxbows and pools in and nearby the river forelands. In the centre and the north of The Netherlands, peatland marshes are of great importance. In the eastern part of the country, the species is found in half-open landscapes with small patches of forest and some open water. On the real map of 1994 (not shown), the distribution of the species reflects the availability of suitable habitat in The Netherlands, especially in the western and central parts of The country. In the northern, eastern and southern parts of The Netherlands not all suitable habitat is occupied so far: a further increase can be expected here.

In all habitats, nest locations are chosen in the rough parts of the landscape, i.e. near water for safety and near grassland for feeding. Nesting birds are found on ground nests, in pollarded trees, and in trees in old nests of other larger bird species such as the common buzzard *Buteo buteo*, the magpie *Pica pica*, the carrion crow *Corvus corvus*, and sometimes on church towers, in colonies of grey heron *Ardea cinerea*, and on artificial nests prepared for the white stork *Ciconia ciconia*. This wide range of nest sites in The Netherlands is the same as that in Africa (Pitman, 1965).

Increase in the number of breeding birds

After the first successful breeding attempt in 1967, the number of breeding birds increased rapidly. In 1972, seven pairs were observed and in 1977 the number was estimated at forty-eight pairs (Teixeira, 1979; Lensink, 1996). Six years later, it had increased to about 111 pairs (SOVON, 1987; Lensink, 1996). During the following years, the number rose further to about 318 pairs in 1989 and 1174 in 1994. After its first settlement in the province of Drenthe in 1983, the numbers there increased to about thirty-two pairs in 1989 and to seventy pairs in 1994. In 1989, a total of about 345 pairs were breeding in The Netherlands and in 1994 about 1340 pairs (Lensink, 1996). After settlement in both areas, growth was exponential (Fig. 4). Up to 1977, the rate of increase for the settlement near The Hague was higher than in succeeding years (test on slope, $t=7.861$, d.f.$=6$, $P<0.001$). From 1976–77 onwards, the species spread over

TABLE 1. Observed velocity C of range expansion of the Egyptian goose for the settlement of The Hague in various periods and for Drenthe. Correlation coefficient r for the relation between the square root of the area occupied and time; the significance level is indicated as *$P<0.05$, **$P<0.01$, ***$P<0.001$.

Settlement	Period	C	n	d.f.	r	Sign.
The Hague	1967–94	3.04	7	6	0.933	***
The Hague	1967–77	1.16	4	3	0.936	***
The Hague	1977–94	4.59	4	3	0.956	*
Drenthe	1983–94	2.83	3	2	0.958	*

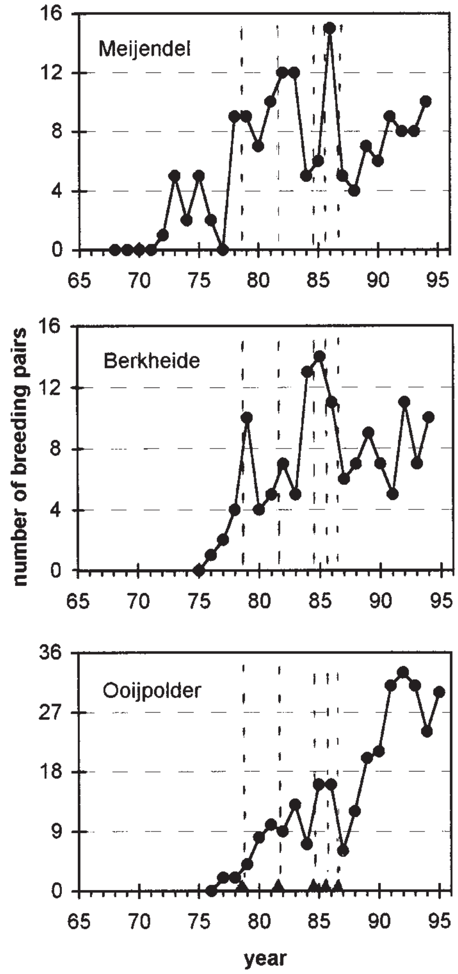

FIG. 5. The number of breeding Egyptian goose in three areas in The Netherlands in 1965–95; see Fig. 1 for the location. Severe winters are indicated with an arrow.

the country (Teixeira, 1979). Before 1977, in all areas, the number of birds probably increased. After 1977 it stabilized in the area of first settlement, and at the same time it increased in both the newly colonized areas in the expansion wave and in the new foci. In Drenthe, from 1989 onwards, pairs were found outside the area of first settlement, up to a distance of 40 km.

In the first years the breeding number increased in small areas, after which it stabilized. For example, in two dune areas near The Hague occupied in the 1970s, the numbers increased to nine pairs and ten pairs in 1979 (Fig. 5a, b). After that, they fluctuated between five and fifteen pairs and five and fourteen pairs, respectively. Elsewhere in The Netherlands, such as in the east along the River Rhine (Ooypolder, Fig. 5c), the stabilization in breeding numbers was also observed. Here the increase in numbers stagnated during 1981–87. In 1987 the number of pairs dropped. After this period, they rose to twenty-three to thirty-three in 1991–95. In both the dune areas, the number of breeding pairs did not fall in 1979 after the very severe winter of 1978/79, but only in 1980. This suggests that in both areas mainly first–year birds suffered from the severe winter of 1978/79. This is only partly confirmed after the severe winters of 1984/85–1986/87. In Meyendel the numbers dropped in 1987 and 1988, in Berkheide in 1986 and 1987, and in the Ooypolder in 1987 (Fig. 5). In the area last mentioned, the results also suggest heavy starvation among adult birds due to the severe winter 1984/85.

Breeding success

Along the rivers in the eastern part of the country, breeding pairs had on average 2.2 young (Table 2). This is the average when the young are 6–8 weeks old, just before fledging (Eltringham, 1975; Cramp & Simmons, 1977). Before this time, about 20% of the birds were lost ($n=20$). Successful pairs had, on average, 5.4 young after 6–8 weeks. In the dunes in the west of The Netherlands breeding pairs had on average 1.6 young, and the successful pairs 3.8. In the previous weeks, about 15% of the birds were lost ($n=12$). The average number of young along the rivers differs from that in the dunes (all pairs, Mann–Whitney U-test, $z=-0.8348$, d.f.$=209$, $P<0.01$, successful pairs, t-test, $t=5.337$, d.f.$=83$, $P<0.001$).

Dispersal of new breeding pairs

Analysing the distribution maps of the Egyptian goose in the eastern river area shows that of the colonizing pairs, 87% were found at a distance of less than 10 km from the range occupied previously (Table 3). The maximum distance was about 45 km. However, in The Netherlands, there also have been birds breeding in places at a greater distance from their birthplace. For instance, in 1977, the first breeding in the eastern river area was found at a distance of more than 100 km from The Hague (Fig. 2). In 1983, in the peatland marshes near the mouth of the River IJssel, the first birds were breeding at a distance of about 75 km from the nearest breeding places. So, the distances found in the eastern river area (Table 2) do not cover the full range of dispersal distances. Table 2 also gives an assumed range, with 80% of the new breeding pairs at a distance of less than 10 km of the place of birth, and a few birds found at distances greater than 50 km.

The number of Egyptian goose in winter

Along the Rivers Rhine, Waal, IJssel, and Meuse in 1974 the species was observed for the first time. From 1976 the birds were seen every winter period and from 1977 onwards every month from September to April, during which time the counts were carried out. Up to the season 1978/79, the numbers showed a constant increase (Fig. 6). During the next season the number stabilized after which a further, but slower, rise in numbers was noticed until 1984/85. In the next 2 years, more or less the same number was recorded. In the following seasons the numbers increased rapidly again, up to a (temporary) maximum in the last season of 1994/95. Stagnation in population growth therefore occurred in three cases, each after a severe winter (1978/79, 1984/85, 1985/86). For unknown reasons, a similar effect of

TABLE 2. Breeding success of the Egyptian goose in two landscapes in The Netherlands. The percentage of success is expressed as the number of pairs with at least one young fledged divided by the total number of pairs, the average number of young fledged is given for all pairs and for the successful pairs.

Area	Period	*n*	% success	Number of young fledged	
				All pairs	Successful pairs
Rivers	1982–94	118	39.4%	2.19 ± 2.90	5.44 ± 1.96
Dunes	1978–94	97	40.2%	1.57 ± 2.22	3.80 ± 1.87

TABLE 3. Dispersal distance (km) of new breeding pairs and the square root of the variance of the dispersal distances σ. The variation is given for the area along the Rivers Rhine, Waal and IJssel in the eastern part of The Netherlands as estimated in the field and an assumed variation (see text).

Class	0–10	11–20	21–30	31–40	41–50	51–100	100–200 km	σ
Rivers	126	11	5	1	1	0	0	6.45
Assumed	126	15	7	5	1	1	1	18.69

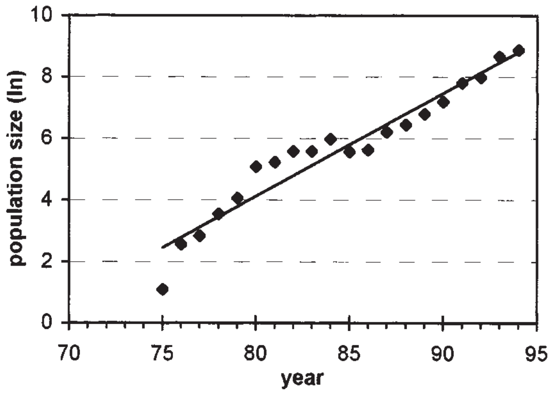

FIG. 6. Increase (ln scale) in numbers of the Egyptian goose during regular counts of waterfowl along the rivers IJssel, Rhine, Waal and Meuse in The Netherlands. The numbers for each month during a winter period (Sept.–Apr.) are added together to a total for the whole season. 1970 stands for the season 1970/71, etc. Line is fitted by means of least squares.

the severe winter 1986/87 does not show up from the figures. This may suggest the operation of natural selection. The relative annual increase is less after (very) severe winters (V>28) than in normal or (very) mild winters ($t = 3.713$, d.f. = 16, P<0.01). The same was found for winters with more than seven icy days compared to winters with 0–6 icy days ($t = 3.727$, d.f. = 16, P<0.01). These results suggest heavy starvation during severe winters, which will lower the number of birds that can contribute to population increase and range expansion. Besides, the numerical increase in numbers outside the breeding season is synchronous with that of the breeding birds along the large rivers (Fig. 5).

Within the winter period, the highest number of Egyptian goose are recorded in November/December (Fig. 7). In mild and moderate winters with a severity index V<28, the number of geese found in January and February dropped slightly (0–20%) (Fig. 7). During severe winters when V>28 they dropped enormously, up to 60% in 1985–86. The seasonal pattern in severe winters differs significantly from that in mild and moderate winters ($\chi^2 = 16.19$, d.f. = 7, P<0.05). Since the Dutch birds are mainly residents (Lensink, 1996), the main factor will be heavy starvation during these severe winters.

Calculation of the range expansion

Range expansion is calculated for various options, in which the survival of *1Y* birds and adults are varied, together with the number of fledged young and dispersal distances. The survival of *1Y* birds varies between 0.5 and 0.7, and the survival of adult birds between 0.5 and 0.9. For the average number of young the value was taken as recorded in the eastern river area in 1984–94 (Table 2). The average number of young in the dune area was lower. In all areas studied, the breeding success was determined some years after the first settlement. It is known that after the first settlement breeding success decreases after a few years, due to density-dependent effects, as has been found for the barnacle goose on Gotland (Larsson & Forslund, 1994). This is why the model has been applied to two options in the number of young, i.e. 1.0 fledged female per year as an average for areas occupied relatively long ago, and 1.25 fledged females as a country-wide average, including the wave of expansion and recently occupied foci. In the various options, the calculated velocity of range expansion varied between 0 km per year and 4.6 km per year. If *1Y* survival is 0.6 and the >*1Y* survival is below 0.70 there is no expansion, because the lifetime reproduction R_o becomes less than 1.0. If *1Y*

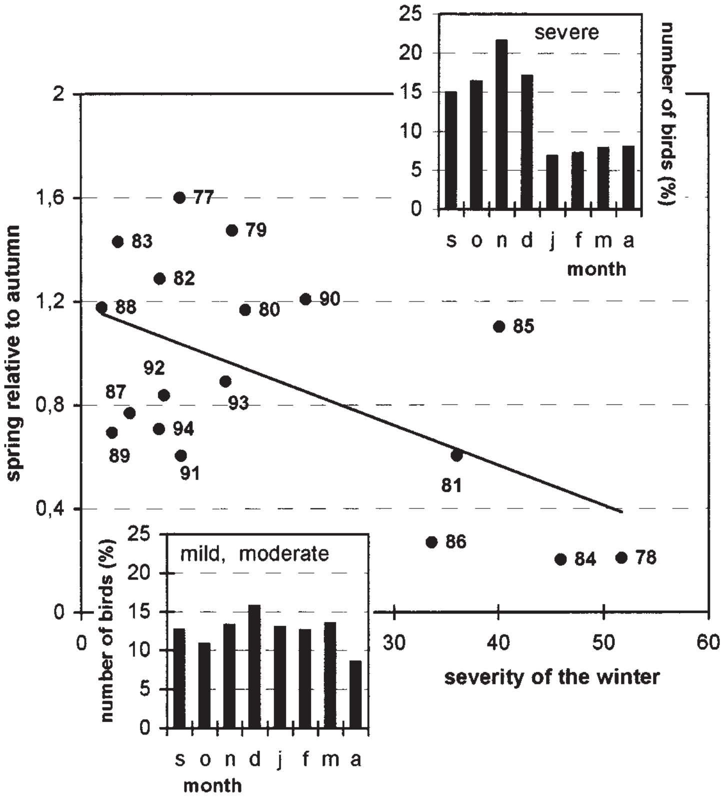

FIG. 7. Relation between the severity of the winter and the number in spring relative to autumn, as well as the seasonal pattern of Egyptian goose along the Rivers Rhine, Waal, IJssel and Meuse during mild and moderate winters, and during severe winters (1978/79, 1981/82, 1984/85, 1985/86, 1986/87). Counts are carried out between September and April.

survival is 0.7 or more, the velocity of expansion ranges from 2.0 km per year with an adult survival of 0.7 up to 3.6 with an adult survival of 0.9. In the most optimistic survival scenario, the calculated velocity (Fig. 8) is about the same as the observed velocity in 1977–94 (Table 1). If the dispersal distances as estimated in the field ($\sigma = 6.45$, Table 3) are applied, the calculated velocities are *ca.* 100% lower.

Calculation of population growth

The matrix model is used for calculating the population growth for various options in the survival of *1Y* and adult birds and for two options in the average number of fledged females. The calculated number of breeding females in the settlement of The Hague varied between thirty-two and 234, although in the field nearly 1200 pairs were counted in 1994 (Fig. 4). If we start the calculation with two pairs in 1969, as Teixeira (1979) mentions, the calculations become more realistic. From the various options calculated (Fig. 9), it becomes clear that adult survival of 0.85 seems to be be realistic, and one of 0.7 for *1Y* birds. In these cases, an observed total of 1150 breeding pairs in the settlement of The Hague and its foci is realistic. Furthermore, when feeding these survival rates into the model, between thirteen

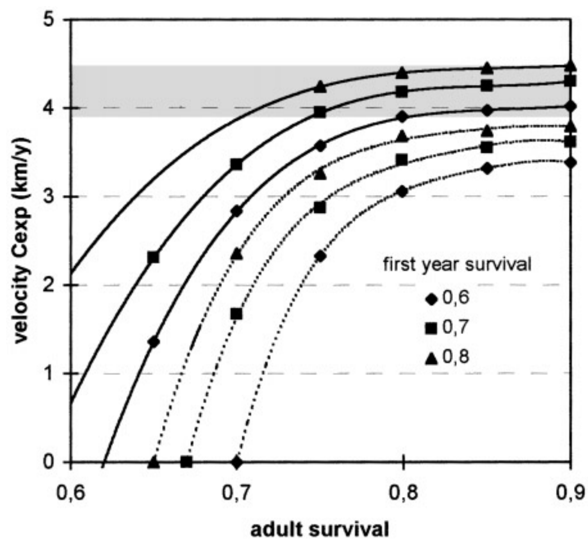

FIG. 8. Velocity of range expansion *C* (km per year), as calculated with the model, for various options in juvenile survival (0.6, 0.7 and 0.8), adult survival (*x*-axis), the number of juveniles fledged (1.0 broken lines and 1.25 solid line), and for dispersal $\sigma = 18.69$ (see Table 3). The observed velocity 1977–94 is marked in grey.

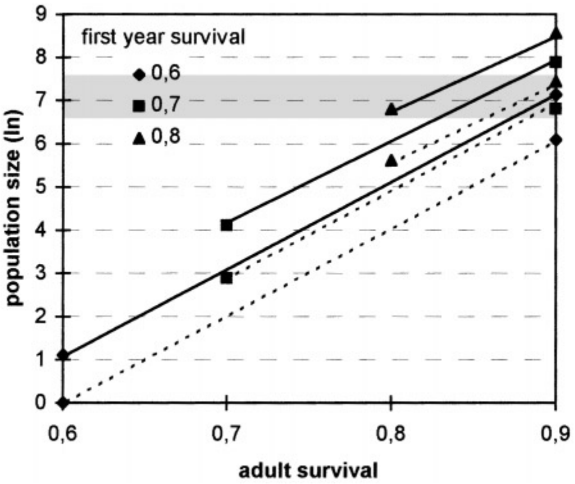

FIG. 9. Population size (number of breeding female Egyptian goose, ln scale) calculated with the population matrix for various options in juvenile survival (0.6, 0.7, 0.8), adult survival (x-axis) and the number of juveniles fledged (1.0 broken lines and 1.25 solid lines). The observed population size in 1994 is marked in grey.

and fifteen pairs can be expected to have bred near The Hague. Thus, it is clear that the population grew quickly in the period 1967–77 (Fig. 4). There are indeed reports of high numbers of juveniles per pair during these years (Teixeira, 1979). Apart from this, it is also possible that in the first years renewed escapes from city parks took place. For example, around 1967 more birds escaped in these areas (Lever, 1967; Teixeira, 1979). According to the model, in the settlement at Drenthe only a few pairs were expected to breed after 12 years. In the field, in 1994, a total of seventy pairs was counted. Here, in parks in the city of Groningen, birds still raised young after 1983, which joined the feral population in Drenthe after fledging (Lensink, 1996). Apart from this, in Drenthe very good breeding success during the first years might also have been a crucial factor in Drenthe, as with the settlement of The Hague.

DISCUSSION

Data collection

Various sources were used for both compiling the distribution patterns and estimating a realistic number of breeding pairs in different years. All data concern probable or confirmed breeding (Sharrock, 1974; Bibby *et al.*, 1992). In western Europe, both have been proved to work accurately for the estimation of the real number of breeding geese (Tomialojc, 1980; Hustings *et al.*, 1984; Bibby *et al.*, 1992). Also during the breeding season, the Egyptian goose has a striking appearance, makes much noise and is often seen fighting with nearby pairs or with other species for nest sites (Cramp & Simmons, 1977; Brown *et al.*, 1982). If the species is present, it is therefore hard to miss. Mistakes in my distribution maps and breeding numbers are therefore considered to be small.

Past and present distributions

In Africa, the Egyptian goose lives in the tropics and subtropics south of the Sahara, as well as in the Nile Valley (Brown *et al.*, 1982; Goodman & Meininger, 1989; Del Hoyo *et al.*, 1992). In ancient times it also inhabited the Mediterranean region (Brown *et al.*, 1982). Since more than hundred years ago a small, but increasing feral population has inhabited England (Norfolk) (Sharrock, 1974; Sutherland & Allport, 1992; Gibbons *et al.*, 1993), where the birds live at the same latitude as in The Netherlands. The geese are residential in this part of Europe. Mainly near Brussels, Belgium, a small feral population amounting to 100 pairs in 1994 has developed since 1974 (Anselin & Devos, 1991; Anselin & Devos, pers. comm.). These birds originated from the Egyptian goose held in the Royal Gardens in Lanaken near Brussels (Devillers, 1988). Because of the absence of birds in the regions between The Netherlands and Belgium, it appears that the species is resident in both countries (Lensink, 1996), there being hardly or no exchange between the two populations. For this reason the Belgium birds were excluded from this study. It is interesting that such a (sub)tropical species could colonize three countries in a temperate climate zone successfuly. In the area covered so far the average winter temperature is a few degrees above 0°C, whereas temperatures in its original, African distribution range are 10–15° higher in the coldest month.

Life-history parameters

Of the life-history parameters needed in both models juvenile and adult survival is not known, but could possibly be estimated. This is why the models were applied with various options regarding survival. For some options the results fitted quite well for both models, using the observed velocity of range expansion and the estimated population size in 1994, i.e. a juvenile survival of about 0.7 and an adult survival of about 0.85. For a closely related species, the somewhat smaller shelduck *Tadorna tadorna*, a mean annual survival of 80% for adults has been found (Cramp & Simmons, 1977). For goose species of a similar size to that of the Egyptian goose, such as the dark-bellied brent goose *Branta bernicla* or the barnacle goose *Branta leucopsis*, the annual survival rates of the adults are 84% (Ebbinge, 1992) and 90% (Ebbinge *et al.*, 1991), respectively. The survival of first-year waterfowl is always lower (see Cramp & Simmons, 1977). A survival rate of 85% for *>1Y* Egyptian goose therefore seems likely to be a good estimate, and *ca.* 70% for *1Y* birds. In this case, the calculated velocity of range expansion is between 3.6 and 4.2 km per year (Fig. 8) and the calculated population size between 900 and 1100 pairs (Fig. 9), depending on the number of goslings fledged.

To explain the success of Egyptian goose in Europe we can search for possible differences in the survival of *1Y* and *>1Y* birds, as well as at the breeding success relative to that in Africa. From the studies of Eltringham (1973, 1974) on the Egyptian goose in Uganda, it follows that the average number of fledgings is less than 2.0. and juvenile survival in the first 2 months is *ca.* 60%. Both figures are lower than observed in The Netherlands. They can be explained by a higher number of (potential) terrestrial and aquatic predators present in Africa. Moreover, one can imagine that with high numbers of large eagle species (Eltringham, 1974), which are very rare in western Europe, the predation pressure among adults in Africa could also be higher.

Based on ringing recoveries in South Africa, Egyptian goose wander long distances outside the breeding season (Oatley & Prŷs-Jones, 1986). Of all birds 98% were recovered within distances of 1–1000 km from the place of ringing. The movements of the species were mainly induced by the annual cycle in rainfall in relation to the occurrence of green pastures as feeding sites (Eltringham, 1973; Brown *et al*., 1982). However, the use of these South African dispersal figures is not realistic. In The Netherlands the species does not wander such great distances as it does in Africa (SOVON, 1987; Lensink, 1996). In fact, the whole country has good feeding opportunities, so that there is no need for movements over long distances. Secondly, outside the breeding season, birds often behave differently from their behaviour during the breeding season. Due to the lack of dispersal data based on ringing, an alternative method was used. Although we have no idea of the real age of birds in new settlements, is seems acceptable that mainly *2 Y* birds breed here.

Model of range expansion

In most analyses of range expansion in birds, a linear relationship has been found between the square root of the area occupied and time (Okubo, 1988; Hengeveld, 1989; Hengeveld & Van den Bosch, 1991; Van den Bosch *et al*., 1992). This relationship also exists in insects (Elton, 1958; Hengeveld, 1989; Andow *et al*., 1990a; Nash, *et al*., 1995) and mammals (Skellam, 1951; Lubina & Levin, 1988; Reeves & Usher, 1989; Van den Bosch *et al*., 1992). For birds, this relationship is linear only after an initial phase. During this phase, the population builds up before it expands. The length of this phase varies between years for small species such as the starling and the house sparrow and more than 10 years for larger species such as the cattle egret and the collared dove (Van den Bosch *et al*., 1992). In the relationship between the square root of the area occupied and time for the Egyptian goose, the initial phase is hard to distinguish from the phase of constant spread (Fig. 3), although in the first years the slope of the curve is clearly less steep. Fig. 3 shows that the number of birds rose steeply to 1977, and later more shallowly. In both periods, the relationship between numbers and time gives a straight line. We can interpret the period to 1977 as the initial phase of population build-up. In this period the spread was slow, becoming faster during the phase of constant spread (Fig. 4). Thus, at the settlement in The Hague, in The Netherlands, the initial phase before the expansion of the Egyptian goose lasted *ca*. 10 years. At the settlement in Drenthe, the main expansion started around 1990, seven years after the first breeding attempt here.

The model used in this study for analysing the range expansion of the Egyptian goose predicts that an organism disperses through the environment by a travelling wave of constant speed (e.g. Fisher, 1937; Skellam, 1951; Okubo, 1980). In theory the area covered in successive years should be a series of expanding circles. To what extent this type of model of biological invasions describes the spread of real organisms depends on two main factors. In reality, ranges are not homogeneous because habitat qualities differ, suitable patches of habitat are not present everywhere and barriers to dispersal can occur. Secondly, dispersal is not simply a travelling wave. Apart from this dispersal at a local scale, long-distance dispersal also occurs. This results in new foci far ahead of the main travelling wave (Hengeveld, 1989; Levin, 1992; Hengeveld, 1994). Moreover, in The Netherlands expansion followed the pattern of suitable habitats present. The Rivers Rhine, Waal and IJssel seemed to form the main corridors for the spread across the country. Along these rivers there are river forelands with a combination of oxbows, pools, claypits and grassland. On the other hand, in 1977 pairs were found breeding in isolated patches of good habitat, for instance in the peatland marshes at a distance of 30 km from the range occupied in this year near The Hague (Fig. 2, 1977). These settlements became foci for later spread, which in subsequent years spread out, coalescing with the main travelling wave.

The model of Van den Bosch *et al*. (1990) is based on survival, reproduction and dispersal at the level of the individual bird. In this study, data from the colonized country itself were used as much as possible. As long as the species in the region of origin behaves similarly to the colonized region, one can use data from the region of origin. In most cases, however, life-history parameters differ between them (Van den Bosch *et al*., 1990). Of the three parameters used, variation in dispersal is most important for explaining differences in the results of the calculations. Although long-distance dispersal concerns spatially rare events, it will lead to new foci. New foci can speed up the overall expansion velocity (Van den Bosch *et al*., 1990, Hengeveld, 1994). This is why the model using dispersal as estimated in the field was chosen, as well as an assumed dispersal as based on experience, since 1967, with the species in The Netherlands (Table 3, Fig. 8).

In absolute terms the observed (3.0 km per year) and the calculated velocity (3.5 km per year) of range expansion are more or less similar, differing *ca*. 20% (Table 1 and Fig. 8). In the study of Van den Bosch *et al*. (1992) calculated velocity of range expansion varied between 10.2 km per year (house sparrow in the U.S.A.) and 135.2 km per year (cattle egret in U.S.A.). The difference between the observed and calculated velocities ranged from −39% (house sparrow in the U.S.A.) up to +50% (collared dove in Europe). The velocity of range expansion of the Egyptian goose is relatively low. The differences between the calculated and observed velocities are in all cases of the same order of magnitude.

Model of population growth

The application of the model for population growth is based on two life–history parameters reproduction and survival. For the first of those parameters, the best available data were used, whereas for the second, guesswork was necessary.

The results show that during the first years the observed population growth was far more than expected from the model. In these first years the population was limited to the vicinity of The Hague. In winter, this is a relatively warm part of The Netherlands, due to the relatively warm North Sea at a distance of only a few kilometres. Compared with regions more inland within The Netherlands, the birds have to deal with frost only in very severe winters. In general, in the 1970s The Netherlands experienced very severe winters in 1969/70 and in 1970/71. Thereafter, up to 1978/79, winters were not (very) severe, but moderate or mild to very mild. The winter of 1974/75 was the mildest of the twentieth century. Since winters are probably important for the survival of Egyptian goose, this mild period was favourable for its fast increase in numbers. From 1976 onwards the species spread rapidly over the country. However, because the species spread inland increasing numbers of birds now had, even in normal winters, to deal with frost. A negative effect on the population growth was noticed because of the very severe winters of 1978/79 and 1984/85–1986/87 (Figs. 5, 6, 7).

Compared to other bird species, geese have a high survival rate in general and a low rate of reproduction (Cramp & Simmons, 1977). This means that differences in survival are of greater importance for the outcome than differences in reproduction. Around 20% of the sensitivity is linked with reproduction and 80% with the survival of the various age classes together. Application of the same survival rates with English data on breeding success (less than 1.0 fledgling per year, Sutherland & Allport, 1992) gives a stable to a very slowly growing population. This outcome reflects the current situation reality in Britain (Gibbons *et al.*, 1993; Delany, 1993).

Prospect

At present, the Egyptian goose continues to colonize The Netherlands and Belgium and it has started to colonize Germany across the Dutch borders. In the lowlands east of the North Sea, even in the coastal areas of France, there is plenty of suitable habitat for the species. In the south, the Dutch and Belgian populations will meet within a few years, after which they will probably expand further south into France. I expect that in Germany it will expand further towards Denmark across the Rivers Eems, Wezer and Elbe and towards the south east along the Rhine and its tributaries. At around these geographical limits, I expect the colonizisation process to stop because of the severity of the winters, probably at the 0°C isotherm equalling diurnal temperatures below 0°C for all of January. Based on the recorded effects of severe winters on juvenile and adult survival in The Netherlands, this seems to be a realistic option. Also, cold weather in March has a negative effect on the breeding success of the Egyptian goose (Kear, 1990). Fig. 8 shows that in the case of a survival rate of 60% for *1Y* birds and less than 70% for adults, the lifetime number of fledglings R_o comes below 1.0. In this situation, there will be no more population growth and range expansion.

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First of all I thank Rob Hengeveld and Frank van den Bosch for the discussions we had on the subject and the comments they gave on earlier drafts. Secondly, I thank Jan van Gelder, my supervisor at the University of Nijmegen, for his critical questions on birds in general and on animal range expansion in particular. I also thank Bart Ebbinge, Robert Kwak, Leon Lamers, Jan van Groenendael and Theo Verstrael for useful remarks on earlier drafts. Finally, Rob Hengeveld kind enough to correct my English. Johan Bekhuis, Fokko Erhart and Theo Verstrael kindly supplied data on the breeding success in their region. Johan and his co-workers supplied maps with the breeding bird distribution in different years. From their databases SOVON and Central Bureau Statistics Netherlands (CBS) made the data on the Egyptian goose available. Ward Hagemeijer prepared the distribution maps. Ivo Duynstee helped with the calculations of matrices.

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BIOSKETCH

One of the fascinating things of bird census work is the year to year variation in abundance and distribution of bird species. During my study I made a reconstruction of the colonization of The Netherlands by exotic bird species (*Limosa* **69,** 103–130). Further interest in the process of colonisation got me in contact with Rob Hengeveld and Frank van den Bosch. Based on their ideas and models (*J. Biogeogr.* **15,** 135–150), I analysed the recovery of raptors in Great Britain and The Netherlands after the pesticide crash of the sixties (*J. anim. Ecol.* **66,** 811–826) and the expansion of the Egyptian goose *Alopochen aegyptiacus* in The Netherlands (this paper).