Has the recent breeding range expansion of Arctic geese been facilitated by changes in human land use?


Summary

1. As in many Arctic breeding herbivorous waterfowl species, Barnacle Geese recently showed a strong increase in population size. We have observed a dramatic expansion of their breeding range from the traditional areas in the Russian Arctic to temperate areas in western Europe traditionally used as wintering grounds.
2. We investigated the habitat characteristics of the new nesting and nearby foraging sites in the Baltic and in the Netherlands by means of a questionnaire addressed to nature conservation agencies, farmers and researchers.
3. New nesting sites are mainly situated on small islands, safe from fox predation. Human interference and livestock grazing is usually absent. In contrast, foraging sites used during chick rearing are typically found at the mainland and are grasslands with a short sward, most often grazed by livestock or subjected to a mowing regime.
4. There are no overall changes in land use that explain the breeding range expansion of the Barnacle Geese to the Baltic. New breeding colonies in the Russian Arctic were established following the abandonment of human settlements in these areas. In contrast, the new sites in the Netherlands became available after human land reclamation, dam building and intensification of agriculture.
5. We expect that the growth of the temperate breeding population of Barnacle Geese will level off after recent period of geometric growth as predator-safe nesting sites will become limiting and density-dependent processes will act on the established colonies.
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Introduction

Traditionally Barnacle Geese, *Branta leucopsis*, breed in the high Arctic on the islands of Greenland, Spitsbergen, Novaya Zemlya and Vaygach. Since the 1970s, the Russian population of Barnacle Geese has increased dramatically from about 25,000 geese in 1970 to about 400,000 at present (Figure 10.1). Along with the geometric population growth, Barnacle Geese have also expanded their breeding range. In 1971, the first breeding colony was established in the Baltic Sea, formerly used only as a stopover site during migration (Larsson et al. 1988). The number of geese breeding in these new colonies increased rapidly (Forslund and Larsson 1991; Leito 1996; Larsson and Van der Jeugd 1998; Leito and Truu 2004) and at present the Baltic sub-population numbers about 21,000 birds. During summer 1988, the first breeding pairs were observed at traditional wintering sites of this species in the Netherlands (Meininger and Van Swelm 1994; Van Dijk et al. 2005) and numbers here have increased dramatically since then, reaching almost 6,000 breeding pairs in summer 2005, mainly in the southern delta region (Ouweneel 2001; Van Dijk et al. 2005) (Figure 10.1). In 2005, the North Sea population numbered about 25,000 birds in all. Around the same time, in the 1980s, Barnacle Geese expanded their breeding range in Russia all along the coast of the Barents Sea (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995). The colonies in the Baltic, the Netherlands and Russia initially showed geometric growth (Larsson et al. 1988; Mineev and Mineev 2004; Van Dijk et al. 2005). The growth of the Baltic population has levelled off during the past five years, whereas the Dutch population is still increasing (Van Dijk et al. 2005) (Figure 10.1).

During the same period goose populations around the world have increased tremendously. In North-America, the populations of Greater and Lesser Snow Geese (*Chen caerulescens caerulescens*, Abraham et al. 2005) and (*Chen caerulescens atlanticus*, Gauthier et al. 2005) went through a period of population explosion from the late 1960’s to the mid-1990’s. In Japan the population of wintering Greater White-fronted Goose (*Anser albifrons*) increased almost six-fold in a 20-year period (Shimada 2002). In Europe, wintering populations of Pink-footed Geese (*Anser brachyrhynchus*, Fox et al. 2005), Greenland White-fronted Geese (*A. albifrons flavirostris*, Fox et al. 2005), Bean Geese (*A. fabalis*, Van Eerden et al. 2005) and Greylag Geese (*A. anser*, Van Eerden et al. 2005) have increased since the 1960’s. Along with the increase of wintering numbers of Palearctic goose species in Western Europe also the number of exotic species increased and Egyptian (*Alopochen aegyptiacus*, Lensink 1998), Canada (*Branta canadensis*, Van Roomen et al. 2004) and Bar-headed Goose (*Anser indicus*, Van Horssen and Lensink 2000) are now common on grasslands in Europe (Lever 1987). These neozoic populations, probably founded by individuals escaped from waterfowl collections, are non-migratory and have bred successfully in the new habitats (Van Dijk et al. 2005). Concurrently, Palearctic species
Breeding range expansion of Arctic geese

Figure 10.1: Population trend of the East Atlantic Flyway population of Barnacle Geese (triangles) as well as the number of breeding pairs in the more recently established Baltic (open circles, included are birds breeding on the Swedish islands of Öland and Gotland) and Dutch colonies (closed circles).

such as the Greylag and the Barnacle Goose expanded their breeding range towards temperate regions (Forslund and Larsson 1991; Loonen and de Vries 1995; Van Eerden et al. 2005).

Changes in hunting regulations and the designation of refuges for wintering and migrating geese are often mentioned as potential causes of the increase in goose numbers (Ebbing 1991; Menu et al. 2002; Ngai and Jefferies 2004). However, most studies attribute the dramatic increase in goose numbers primarily to changes in human land use, such as increased fertilisation of grasslands, cultivation of wheat, corn and rice (Fox et al. 2005; Abraham et al. 2005; Van Eerden et al. 2005) and changes in harvesting techniques (Shimada 2002). In addition, part of the population increase is assigned to alterations in the foraging habits of the geese such as shifts from traditional foraging on (semi-) natural grasslands to agricultural fields (Ganter et al. 1999; Fox et al. 2005; Gauthier et al. 2005). In North America, strong increases in the number of Lesser Snow Geese on the breeding grounds around Hudson Bay led to severe foraging pressure on natural salt marshes and caused habitat degradation and a loss of salt-marsh habitat (Jefferies and Rockwell 2002; Jefferies et al. 2006). As a consequence, Lesser Snow Geese have shifted their breeding
areas, and it is expected that they will negatively affect their habitat on these new sites as well (Abraham et al. 2005). This quickly growing population uses more and more agricultural fields during wintering and spring staging, causing increasing conflicts with agriculture (Abraham et al. 2005). At present the population of Lesser Snow Geese in North America is under an intense hunting regime, but numbers are still rising (Abraham et al. 2005). Also in other parts of the world, growing goose populations are causing severe conflicts with agriculture and solutions are being sought (Ankney 1996; Batt 1997; Vickery and Gill 1999; Beck et al. 2002; Cope et al. 2003; Amano et al. 2004; Fox et al. 2005; Van der Jeugd and Voslamber 2006).

We conducted a survey of the nesting and adjacent foraging sites of Barnacle Geese in the Netherlands and in the Baltic. In the survey we focused on habitat characteristics and management. Additionally, we provide counts of the number of nesting and foraging birds. First, we will examine habitat parameters required by Barnacle Geese for nesting and gosling rearing at the newly established colonies and compare these with the traditional habitats in the Russian Arctic. Secondly, we will investigate whether land use has changed over the past decades in recently colonised sites, and whether this facilitated the establishment of new colonies. Finally, we will discuss the growth of these new breeding populations in relation to population growth at traditional sites.

**Methods**

**The Netherlands**

Data on the number of geese and their breeding areas was supplied by SOVON Dutch Centre for Field Ornithology. SOVON organises nationwide counts of wild birds in the Netherlands. Fieldwork for these surveys is carried out by volunteer ornithologists. To date, 270 different areas have been recorded in which at least one pair of Barnacle Geese bred for at least one year, but this is likely to be an underestimate. In 17 of these areas more than 10 pairs bred for at least five subsequent years (Table 10.1, Figure 10.2). In the larger areas more than one colony was established and several sites were used as foraging sites. We subdivided the data set into sites and analysed data for a total of 20 nesting sites (1-6 sites per area) and 16 foraging sites (0-2 sites per area). Data on site characteristics (location, size of the site, vegetation description, estimate of canopy height) and management (nature protection measures, accessibility for people, livestock grazing, mowing or fertilisation) were collected using questionnaires sent to local birdwatchers, farmers or site-managers working for nature conservation agencies.

Numbers of nesting and foraging geese were related to the size of the nesting and foraging sites by linear regression analyses. Differences in canopy height between nesting and foraging sites were explored with a two-sample t-test.
For the Baltic area, we relied on detailed surveys of nesting and foraging habitats carried out by K. Larsson and H. van der Jeugd in Sweden and A. Leito in Estonia. Estonia harboured five sites and Sweden 17 sites, each of which had 10 or more breeding pairs for at least five consecutive years (Table 10.1, Figure 10.2). All sites in Sweden used for the analysis were situated along the coast of the island of Gotland. A few colonies at the coast of the Swedish mainland near Stockholm (Forslund and Larsson 1991) and along the coast of the island of Öland were not included in our dataset. For the sites on Gotland, we distinguished mainland sites, situated on Gotland main-island as opposed to the smaller islands along the shore. In Sweden, annual counts of nests were made from 1971 onwards, during the same period numbers of adults and young were counted at the annual wing moult at the end of July on the foraging sites. The most recent counts (2005) of these nesting and foraging geese were related to the size of the nesting and foraging sites by means of linear regressions. In Estonia nest counts were conducted in the period from 1981-2002 by A. Leito. Differences in canopy height between nesting and foraging sites were explored using a two-sample t-test.

Figure 10.2: The East Atlantic flyway with the breeding grounds of the Barnacle Goose (shaded area) and, in more detail, the newly established breeding areas in the Baltic Sea (Gotland, \( N =17 \) and Estonia, \( N =5 \)) and in the Netherlands (\( N =14 \)).
Table 10.1: Number of breeding areas and the number of sites used for the analyses in this study

<table>
<thead>
<tr>
<th></th>
<th>Total number of breeding areas</th>
<th>Total number with &gt;10 pairs</th>
<th>Number of areas used in analysis</th>
<th>Number of sites used in analyses</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Nesting sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estonia</td>
<td>24</td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Sweden</td>
<td>&gt;44</td>
<td>17</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>The Netherlands</td>
<td>270</td>
<td>17</td>
<td>14</td>
<td>20</td>
</tr>
<tr>
<td><strong>Foraging sites</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Estonia</td>
<td></td>
<td>5</td>
<td>5</td>
<td>5</td>
</tr>
<tr>
<td>Sweden</td>
<td></td>
<td>17</td>
<td>17</td>
<td>17</td>
</tr>
<tr>
<td>The Netherlands</td>
<td></td>
<td>15</td>
<td>16</td>
<td>16</td>
</tr>
</tbody>
</table>

Figure 10.3: Site choice of Barnacle Geese for nesting and foraging in Estonia (black bars, nesting $N = 5$, foraging $N = 5$), Sweden (white bars, nesting $N = 17$, foraging $N = 17$) and the Netherlands (grey bars, nesting $N = 20$, foraging $N = 16$): (A) location, (B) conservation status (C) accessibility to people (D) grazing or mowing
Results

Almost all breeding colonies in the Baltic, as well as in the Netherlands, are situated on islands (Figure 10.3A), within nature reserves (Figure 10.3B) and are not accessible to people during the breeding season (Figure 10.3C). About half of the islands are grazed by livestock or managed by mowing (Figure 10.3D). Foraging sites are more often found on the mainland and in places that are accessible to people (Figure 10.3A,C). A large proportion of these sites is grazed by livestock or mown for haymaking (Figure 10.3D). Nesting habitats can be very diverse, ranging from bare stony beaches to dense scrub or bushes. Foraging habitats, in contrast, almost always comprise grasslands (Figure 10.4). Average canopy height of the nesting sites is higher than that on the foraging sites (two-sample t-test: Sweden $t_{32}=1.93$, $P=0.03$; the Netherlands $t_{34}=3.3$, $P=0.001$; Figure 10.5). All nesting and foraging sites were situated in the close vicinity of water bodies. Table 10.2 summarises the average conditions of nesting and foraging sites.

![Figure 10.4: Habitat types at nesting and foraging sites in Estonia, Sweden and the Netherlands.](image-url)
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Figure 10.5: Canopy height for nesting and foraging sites in Estonia (black bars), Sweden (white bars) and the Netherlands (grey bars). Different letters indicate significant differences.

For Sweden we found a positive relation between the size of the nesting sites and the number of breeding pairs at the site ($R^2=0.37$, $P=0.01$). Here we also detected a strong positive correlation between the size of the foraging site and the number of adult geese counted at the site by the end of July ($R^2=0.83$, $P<0.01$; Figure 10.6A). The slope of this regression line reveals that the capacity of foraging sites in Sweden is about 20 geese ha$^{-1}$.

For the Netherlands, we did not find a significant relationship between size of the nesting sites and the number of breeding pairs at these sites ($R^2=0.19$, $P=0.06$), nor between the size of the foraging sites and the number of geese on these sites ($R^2<0.001$, $P=0.99$; Figure 10.6B). A better fit might be obtained if more sites and other species of breeding geese were included.

Figure 10.6: Number of foraging geese and goslings in relation to size of the foraging site for (A) Gotland ($R^2=0.83$, $P<0.01$) and (B) the Netherlands (regression n.s.).
Most areas in the Netherlands where geese are nesting (11 out of 14 areas) are islands that came into existence after tidal influence was reduced by the building of dams for flood prevention works. In the Baltic, we do not have any indications of changes in land use that might have facilitated the establishment of goose colonies.

Discussion

Contrasting habitat requirements of nesting and foraging geese

Barnacle Geese can nest in a wide variety of habitats. Traditional breeding areas along the coasts of Novaya Zemlya and Vaygach Island, as well as those on Greenland and Spitsbergen, comprise cliff ledges, rocky outcrops and small islands (Ganter et al. 1999). Here the cliffs and the overall isolation of the islands provide safety from ground predators. Traditionally, avian predators mainly predate on goose eggs and chicks in years when few lemmings are around. In such years predation by birds of prey and especially gulls, and in some colonies also by foxes, reduces breeding success to virtually nil (Syroechkovsky et al. 1991; Mainguy et al. 2002). More recently established nesting sites in the Russian Arctic along the coast of the Barents Sea are more diverse; we observed geese nesting on small islands, salt marshes, dunes, tundra and former hayfields (pers. obs.; Syroechkovsky Jr. 1995; Van der Jeugd et al. 2003; Chapter 2). Not only the habitat, but also the nesting substrate, shows a large variation (Litvin and Gurtovaya 2005).

In the Netherlands, Sweden and Estonia we found a wide variety of nesting habitats, from bare stony islands to islands almost completely overgrown with shrubs and trees or tall reed-beds. For nesting sites, clearly the most important requirement is safety from predators, and this is accomplished by nesting sites usually being situated on small islands or on other sites that are inaccessible for ground predators and people. Additionally, a tall canopy on many places prevents detection of the nest from the air by avian predators. Finally, the absence of livestock ensures a tall canopy and decreases the probability of trampling and disturbance of female geese on the nest during the breeding period.

Foraging geese select sites with the highest possible forage quality. Protein requirements of chicks in the early growth phase are at least twice as high as that of adults birds (Murphy 1996). A more nutritious diet positively influences growth rate of goslings, their body size as adults, and, hence, the chance of post-fledging survival and future reproductive success (Cooch et al. 1991; Sedinger et al. 1995; Loonen et al. 1997; Larsson et al. 1998; Van der Jeugd and Larsson 1998; Sedinger et al. 2004). The breeding islands, though safe havens, are in many cases unsuitable for gosling rearing because of low forage availability. Geese leave the nesting sites as soon as the goslings hatch and move to greener pastures. At that time, they prefer short, nutrient-rich grasslands (Sedinger and Raveling 1986; Forslund and Larsson 1991; Stahl and Loonen 1998). This type of grassland is often
maintained by livestock grazing, fertilising and/or mowing (Summers and Critchley 1990; Vickery et al. 1994; Hassall et al. 2001; Van der Graaf et al. 2002; Bos et al. 2005). Safety is still important and explains why all foraging sites of Barnacle Geese are adjacent to water bodies, where the flightless goslings and their moulting parents escape in case of predator attacks or disturbance. Stahl and Loonen (1998) show that in years with foxes present in an Arctic colony on Spitsbergen Barnacle Geese forage only in the proximity of open water. Traditional foraging sites are Arctic salt marshes that reach a peak in nutritional quality around the time of gosling-hatch and the geese have access to high quality forage during the gosling-rearing period (Chapter 5). In natural marshes in temperate regions, the peak in nutritional quality occurs much earlier in spring. Though Barnacle Geese breeding in more temperate regions advanced their laying dates significantly, they have not shifted their laying dates sufficiently to coincide with the peak in the nutritional quality of the vegetation. Instead, the gosling-rearing period is now sub-optimally timed and coincides with a tall canopy and low nutritional quality of the forage (Chapter 5). A similar phenomenon is documented for many other bird species reacting to environmental changes in temperate areas (Visser et al. 2004). Geese compensate for the lower forage quality by foraging in livestock-grazed marshes and agricultural fields, where canopy heights are kept low and nutrient content high by large grazers or even by artificial fertiliser application (Summers and Critchley 1990; Vickery et al. 1994; Hassall et al. 2001; Van der Graaf et al. 2002; Bos et al. 2005).

From our study we can conclude that nesting and chick-rearing geese have different habitat requirements (Table 10.2). Thus, to successfully breed and raise chicks, Barnacle Geese need a combination of safe nesting sites and high-quality foraging sites within reasonable distance from each other.

### Table 10.2: Habitat requirements for nesting and foraging sites of Barnacle Geese, derived from data from the Baltic and Dutch colonies. (n.i. = not important, n.a. = not applicable)

<table>
<thead>
<tr>
<th></th>
<th>Nesting</th>
<th>Foraging</th>
</tr>
</thead>
<tbody>
<tr>
<td>Location</td>
<td>Island</td>
<td>close to water</td>
</tr>
<tr>
<td>Vegetation</td>
<td>n.i.</td>
<td>grassland</td>
</tr>
<tr>
<td>Canopy height</td>
<td>n.i</td>
<td>low</td>
</tr>
<tr>
<td>Management</td>
<td>no livestock</td>
<td>livestock grazing</td>
</tr>
<tr>
<td>Accessibility</td>
<td>not accessible</td>
<td>n.i.</td>
</tr>
<tr>
<td>Size</td>
<td>1-55 ha</td>
<td>3-80 ha</td>
</tr>
<tr>
<td>Distance</td>
<td>n.a.</td>
<td>0-10 km</td>
</tr>
</tbody>
</table>
Changes in land use

In the Baltic area there are no obvious changes in land use that might have triggered the establishment of Barnacle Goose colonies. However, atmospheric nitrogen deposition became obvious in the 1950’s in Scandinavia and undoubtedly affected vegetation throughout the Baltic region. The expansion of the breeding range to the Baltic, therefore, seems to be independent of any obvious population or environmental changes. Breeding range expansions to the Dutch delta area and along the Russian coast around 1990 also appear to be independent events. However, at this time goose numbers increased dramatically in the traditional population (Ganter et al. 1999) as well as in the Baltic population (Figure 10.1). The establishment of the new colonies in the Dutch delta at this time might have been caused by a lower forage availability during the gosling-rearing period due to increased resource competition, and hence a reduced breeding success in the traditional Russian breeding grounds as well as the Baltic breeding grounds (Larsson and Van der Jeugd 1998). In Barnacle Geese, previous work on Spitsbergen, and especially that in the new populations on Gotland have shown that breeding success rapidly declines with increasing population size, due to density-dependent effects on reproduction (Larsson and Forslund 1994; Loonen et al. 1997; Larsson and Van der Jeugd 1998; Drent et al. 1998; Loonen et al. 1998), concomitantly a higher emigration rate has been documented.

The geese that colonised the Baltic Sea encountered a much lower forage quality during the gosling-rearing period than that at their Arctic foraging sites (Chapter 5). At the same time, overall energetic expenses of the geese on an annual balance are strongly reduced as they skip a large part of their migration route, and the prolonged season allows slower growth of goslings without severe penalties. Indeed, gosling growth in these colonies is slower than that in the Russian and other Arctic colonies, although final body size of the goslings is similar due to the longer foraging season (Eichhorn and Van der Jeugd unpubl; Loonen et al 1997).

In the early 1990’s, after the fall of the Soviet regime, many coastal settlements in northern Russia were abandoned. New colonies of Barnacle Geese were established at or near these abandoned settlements soon afterwards (Filchagov and Leonovich 1992; Syroechkovsky Jr. 1995; Van der Jeugd et al. 2003). Although the presence of people (goose hunting and egg collecting) probably prevented earlier establishment of colonies, the long tradition of Arctic fox-hunting in these areas may have counteracted the negative human impact. Geese probably profited from a virtually predator-free environment during the early phase of colony establishment when local fox populations still had to recolonise the surroundings of the former settlements.
In the Netherlands, 11 of the 14 main breeding areas are situated in estuaries in the delta area in the south-west, where three major rivers, the Rhine, Meuse and Scheldt, flow into the North Sea. In 1953, a catastrophic flooding event in the Dutch delta gave rise to the construction of several dams to prevent future disasters. The construction of most of these dams was finished between 1960 and 1987. The dams altered not only the salinity of the estuaries from saline to brackish, but also reduced tidal influences and changed water currents. Many small islands and shoals, on which Barnacle Goose colonies are now established, have emerged during this period. At the same time, agricultural exploitation intensified and nitrogen fertiliser was supplied to grasslands; hence, the quality and productivity of these grasslands increased dramatically (Van Eerden et al. 2005). In addition, high discharges of N and P from agriculture has led to considerable eutrophication of many of the closed sea arms in the Dutch delta area (Oenema et al. 2005). Inundation of foraging sites with these waters has a fertilising effect leading to nitrogen contents of preferred vegetations that are comparable to what is found at the traditional Arctic sites (Pouw et al. 2005). Between 1960 and 1980, we can observe the appearance of suitable nesting sites along with high quality foraging sites in the Dutch delta. In 1988, the first successful breeding pair was observed (Van Dijk et al. 2005) and this was followed by a geometric increase in numbers. At two of the largest (and oldest) colonies in the Dutch delta the first breeding pairs were observed four years after the completion of dams that reduced tidal influence at the sites. The areas that developed after the reduction of tide soon attracted various numbers of breeding birds, thereby gaining the status of nature reserves soon after. The vegetation, which is tolerant of brackish conditions, is usually grazed in summer by cattle (Bakker et al. 1993).

Interestingly, human activities had very contrasting effects on the establishment of new breeding areas for Barnacle Geese, when Russian and north-west European sites are compared. We observed on the one hand that expansion of breeding colonies within Russia is triggered by the abandonment of human settlements, while on the other hand human activities, such as forage quality manipulation and embankment of polders have given rise to new colonies in the Dutch delta.

**Flexibility of migratory routines?**

There is no unifying factor in the newly established breeding sites that can explain the recent overall expansion of the breeding range of Barnacle Geese. We suspect that the increase in the total population of Barnacle Geese probably has heightened exploration of alternative sites. Recent changes in habitat parameters at previously unsuitable sites can partly be attributed to changes in land use that alter predation pressure and forage availability and facilitated the successful establishment of new colonies along the flyway. Sutherland (1998) reviews historic changes in avian migration routes, and tabulates ‘substantial change’ in 12 populations of geese and swans. Excluding the naturalised
species, the shifts in migratory routines entailed a shortening of the autumn migration allowing the birds to winter closer to the breeding areas (two swan populations and five goose populations, to which the Brant, *Branta bernicla nigricans* can be added; this goose species breeds along the Arctic coasts of Alaska and adjoining Canada and now winters in increasing numbers in south-west Alaska instead of migrating to Mexico as in former times, Ward et al. 2005). In these geese and swans with extended parental care, migration routes are shaped by family tradition (‘culturally determined’) and none of the recorded changes result in sub-optimal solutions, this in sharp distinction to other bird groups with short parental care where about half of the changes in migration routes are considered sub-optimal (involving unnecessary detours). For waterfowl there is circumstantial evidence that these alterations in wintering locality (‘short-stopping’) are often directly related to changes in agricultural practice, unintentionally providing crop residues (Owen et al. 1986; Cooke et al. 1995; Gill et al. 1997). Previous research on Barnacle Geese from the Spitsbergen breeding population, suggests that the recent northwards expansion of the spring staging area of this population is also caused by changes in spring temperatures and agriculture (Prop et al. 1998). We conclude that geese are very flexible in their response to environmental changes by adapting their migratory routines. Aside from the migration between breeding and wintering localities we have been considering here, many waterfowl engage in moult migrations: the non-breeders withdrawing to specific sites to renew their flight feathers (Salomonsen 1968). New traditions in use of mouling sites confirm flexibility in these seasonal movements as well (Greylag Geese, see Loonen et al. 1991; Canada Geese, Walker 1970). These opportunistic shifts in mouling sites have implications for breeding range changes. In many documented cases, breeding colonisation by Barnacle Geese followed on a pioneering phase of mouling flocks using the area in late summer in earlier years (Spitsbergen, Drent et al. 1998; Gotland, Larsson et al. 1988; Russia, Filchagov and Leonovich 1992)

**Perspectives**

Currently, the colonies on Gotland seem to have reached a maximum size and numbers are now controlled by density-dependent effects (Figure 10.1). For the Netherlands as a whole we still observe a geometric increase in numbers of breeding birds, although growth is slowed down in the oldest and largest colonies. Continuing growth of the Dutch population will depend on the availability of suitable nesting and foraging habitats, as well as on the carrying capacity of the new colony sites. We have demonstrated that Barnacle Geese breed in a variety of habitats as long as their requirements can be met. Absence of foxes is of prime importance. New nesting sites are therefore either in areas without foxes or on sites that are inaccessible to foxes (Van der Jeugd ms). Fox populations in the Netherlands have been increasing in recent decades and there are now only a few remaining areas with a low density of foxes. Restrictions on foxhunting might halt or even overturn the increase of
breeding Barnacle Geese and other goose species in the Netherlands into a decrease. However, under the current nature management policy in the Netherlands there is some leeway to lift such restrictions locally.

Counts of adult geese and goslings in the newly established breeding colonies in Sweden show that there is a strong relation between the size of the colony and the size of the foraging site. The slope of this line gives the maximum number of geese per unit area; for Sweden this number, 20 birds ha$^{-1}$, is twice as high as the number found near breeding colonies in Spitsbergen (Drent et al. 1998). In the Netherlands we do not detect this relationship, probably because the breeding areas have not yet reached their maximum capacity. It is likely that in the Dutch breeding colonies, as numbers increase, density-dependent processes will act, similar to those in the Baltic colonies. In the Baltic population the number of fledged young per breeding pair decreased dramatically as colonies grew (Larsson and Van der Jeugd 1998). It is therefore likely that we are not facing a continuing increase in populations in the Netherlands, but that a ceiling will be reached when there are no new suitable habitats to colonise and when the existing colonies have ceased to grow. Some of the older colonies in the Netherlands already stopped growing. Until now the establishment of breeding populations of Barnacle Geese in the Netherlands has not resulted in conflicts with agriculture. This is primarily due to the fact that so far, birds have kept to semi-natural pastures, usually within nature reserves. At few sites there is concern for interference by the birds with long-term goals for nature management, e.g. maintaining healthy populations of meadow birds. However, with populations still increasing it is likely that more conflicts, especially with agricultural activities, will arise in the near future. We hope, therefore, that the results and insights presented in this paper may be of some use for finding sustainable, long-term solutions to resolve such conflicts.

**Acknowledgements**

Large numbers of volunteers collected data on geese over the years and filled in the questionnaires in the Netherlands, without their input the analyses would have been impossible to conduct. Vereniging Natuurmonumenten (NL), Staatsbosbeheer (NL) and Länsstyrelsen Gotland (SE) supported our study by supplying data. SOVON (NL), University of Oldenburg (DE), University of Groningen (NL) and Gotland University (SE) provided logistic and financial support.