Rewarding round-trips or tiresome travels?

Comparing migratory and non-migratory lifestyles in barnacle geese

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Chapter 2. Spring phenology affects goose breeding propensity and hatching success especially at higher latitudes

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Chapter 3. Postnatal growth rate varies with latitude in range-expanding geese: The role of plasticity and day length

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Chapter 4. Latitudinal and sex-dependent constraints on timing of breeding and moult in the barnacle goose

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Chapter 5. Circadian and seasonal patterns of body temperature in Arctic migratory and temperate non-migratory Geese

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Chapter 6. Seasonally migrating geese are more active than residents year-round
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Summary

Samenvatting

SUMMARY

Every year, billions of animals make the journey back and forth between distant areas, making animal migration one of the most striking natural phenomena. Migration is most common among birds and the large flocks that fly north in spring, only to be seen again in autumn, have always fascinated people. Bird migration inevitably raises questions and over time, these have changed from simple questions on where birds go to more complex questions such as how they navigate. The most fundamental question remains why birds migrate: What drives birds to undertake such journeys every year? The tilt of the Earth results in seasonally variable conditions in most areas: in winter it is colder and less food is available, while summer brings higher temperatures and more food. Nowhere are these extremes greater than in the Arctic. The Arctic winters provides a harsh environment for birds to survive, but the Arctic summers are a period of high food availability and a relatively low predation risk. The Arctic is therefore a prime breeding area for migratory birds, and waterfowl and waders in particular are known for their migration to the Arctic. For migration to the Arctic to be worthwhile, the benefits must outweigh the costs. By migrating, the birds should therefore ensure a higher survival and/or higher reproductive success than if they stayed in the same area year-round. However, migration itself also comes with costs, such as the energetic costs of flying, and dangers during migration, such as bad weather or an increased predation risk.

The costs and benefits of migration are therefore closely related to the environmental conditions. These conditions are subject to change, which means that the cost-benefit balance of migration can also change. This can lead to changes in bird migrations, including even transitioning to a resident lifestyle when birds stop migrating. The barnacle goose (Latin: *Branta leucopsis*) has shown such a change in lifestyle since the 1980s. Originally, the barnacle goose was seen as a specialist of high-Arctic breeding areas, but barnacle geese now also breed in the Baltic and in the Dutch Delta, on the original wintering grounds. Coinciding with this southward breeding range expansion, barnacle geese adopted different lifestyles: Arctic-breeding geese continue to migrate, while Baltic breeding birds have shortened their migration and Dutch breeding birds have even stopped migrating entirely.

In this thesis, I investigated the costs and benefits of migration to the Arctic by comparing migratory Arctic-breeding barnacle geese with the non-migratory barnacle geese that breed in the temperate regions. Furthermore, I studied activity differences between migratory and resident geese to understand the behavioural adaptations associated with a migratory life.

In the first part of the thesis, I focused on the life stages that take place on the breeding grounds: reproduction and moult. The decision to breed can be of great importance to the breeding success of the population, because when few birds breed, the number of young will likely be low. In **Chapter 2**, I used data of tracked female barnacle geese to investigate

whether there are differences in the breeding propensity of barnacle geese in relation to breeding latitude and onset of spring. The onset of spring (increase in spring temperature and snowmelt) largely determines the food availability for geese, because it determines the onset of growth of the grass that the geese eat. The further north the geese nested, the more they appeared to be dependent on the onset of spring. In years in which spring was early, the breeding propensity was found to be high, but in years with late springs breeding propensity was very low and almost no geese came to breed at high latitudes. This effect was absent for geese breeding at temperate latitudes. The high breeding propensity in the Arctic with early springs may be due to the greater availability of nesting sites and the local availability of food for adult geese. This gives the adults the opportunity to build up body stores for egg laying and incubation and to start nesting. The geese breeding in temperate areas are probably less dependent on the onset of spring, because the current agricultural land use provides the non-migratory geese with suitable food almost all year round, resulting in a high breeding propensity. The food in the breeding areas is also very important for the goslings, which need vegetation with high protein content to grow. In **Chapter 3,** I compared growth rates of goslings in the Arctic (Russia) with goslings in two populations breeding in the temperate region: on Gotland (Sweden) and in the Dutch Delta (Netherlands). The goslings in the Arctic grew fastest, followed by the goslings on Gotland and in the Netherlands. The differences in growth rate could largely be explained by the differences in daylight experienced by the goslings. It is therefore likely that the growth rate of goslings in the Netherlands and Sweden is mainly limited by the available foraging time. Goslings in the Netherlands and Sweden can afford to grow slower, because they experience less time pressure than Arctic goslings. In the Arctic, goslings must be fully grown in time in order to prepare for autumn migration. The adult birds also experience this time pressure in the Arctic. Breeding and moult must be completed in time to allow for fattening up for the autumn migration. In **Chapter 4**, the relationship between the timing of breeding and moult of geese in the Russian Arctic is compared with geese on Gotland and in the Dutch Delta. In general, later breeding birds were found to moult later, probably to avoid overlap between breeding and moult. This was especially true in the Arctic, where the period between breeding and moult was shortest. In addition, the timing of breeding and moult in females appeared to be more strongly linked than in males, and in the Arctic, females appeared to need an 18-day period after breeding before they could start moulting. The female is responsible for incubating the eggs, a period in which it loses a significant part of its body weight and the subsequent moult also costs energy. Because these two energetically costly periods follow each other in short succession, the females may need time to recover from breeding before they can commence moult. It is possible that this makes it more difficult for females to adjust the timing of breeding and moult than for males, which can play an important role in dispersing and adapting to a new breeding area.

In the second part of this thesis, I focused on the behavioural adaptations in barnacle geese associated with Arctic migration. One of the biggest advantages of migrating north is the increasing day length. To be able to use this, geese have to adjust their day-night rhythm. In **Chapter 5**, using body temperature loggers, it is shown that geese rapidly adjust their day-night rhythm to changing light conditions. This allows the geese to take advantage of the additional foraging time provided by the northward migration, potentially facilitating the compensation of the energetic costs of migration. In **Chapter 6**, I used accelerometer data to show that migratory geese are more active than non-migratory geese throughout the year, probably because they need to forage more due to the energetic costs of migration. The increasing amount of daylight in spring, together with the lengthening of days with northward migration, facilitates a higher foraging activity prior to spring migration. In contrast, Arctic geese have to build up body stores for autumn migration under decreasing light and food conditions. In autumn, the migratory geese are therefore active for a longer period outside the daylight period (at night) than the non-migratory geese. We therefore conclude that a migratory lifestyle comes with additional energy costs as well as additional time pressure to compensate for these costs.

Ultimately, we can conclude that both a migratory and non-migratory lifestyle in barnacle geese is currently viable. While there are clearly costs associated with the migration to the Arctic in the form of energy and time, breeding in the Arctic also provides the conditions to cope with these costs. The breeding range expansion of the barnacle goose is in itself a remarkable development. It is likely that human-induced changes (increased food quality through fertilization and decreased predation pressure through pursuit of predators) allowed barnacle geese to breed at lower latitudes (**Chapter 7**). The balance between the advantages and disadvantages of migration can therefore be altered when environmental changes occur. This can also lead to changes in lifestyle, including abandoning a migratory life. Today, humans have a major influence on global land use and climate. The impact of humans on the environment will therefore determine the future of the migratory lifestyle of many birds.

SAMENVATTING

Elk jaar maken miljarden dieren een reis heen en weer tussen verschillende leefgebieden. Migratie is daarmee een van de opvallendste verschijnselen in de natuur. Migratie komt het meest voor binnen vogels en de grote groepen vogels die in het voorjaar naar het noorden vliegen om vervolgens pas weer in het najaar te worden gezien, hebben mensen altijd gefascineerd. De trek van vogels roept onvermijdelijk vragen op en in de loop der tijd zijn deze vragen veranderd van simpele vragen zoals ‘waar gaan vogels heen?’, tot meer complexe vragen zoals ‘hoe vinden vogels de weg?’. Het meest fundamenteel blijft de vraag waarom vogels migreren: Wat drijft vogels om jaarlijks zulke tochten te ondernemen? De seizoenen op aarde zorgen ervoor dat de omstandigheden in de meeste gebieden variabel zijn: in de winter is het kouder en is er minder voedsel beschikbaar, terwijl de zomer juist hogere temperaturen en meer voedsel met zich mee brengt. Nergens zijn deze extremen groter dan in het poolgebied. De poolwinters bieden vogels maar weinig mogelijkheden om te kunnen overleven, maar de poolzomers zijn een periode van grote voedselbeschikbaarheid en een relatief laag predatierisico. Het poolgebied is dan ook bij uitstek een broedgebied voor trekvogels. Met name watervogels en steltlopers staan bekend om hun migratie naar het poolgebied. Om de trek naar het poolgebied de moeite waard te laten zijn, moeten de voordelen groter zijn dan de nadelen. Door te migreren zouden vogels dus moeten zorgen voor een hogere overleving en/of hoger broedsucces, dan wanneer ze jaarrond in hetzelfde gebied zouden blijven. De trek zelf brengt echter ook kosten met zich mee. Zo kost vliegen energie en kunnen er gevaren optreden tijdens de migratie, zoals slecht weer of een verhoogd risico op predatie.

De voor- en nadelen van migratie hangen daarmee dus nauw samen met de omgevingscondities. Deze condities zijn aan verandering onderhevig, wat ervoor zorgt dat ook de balans tussen de voor- en nadelen van migratie kan veranderen. Hierdoor kunnen veranderingen optreden in het migratiegedrag van vogels, waarbij het zelfs mogelijk is dat vogels stoppen met migreren. De brandgans (latijn: *Branta leucopsis*) heeft sinds de jaren ‘80 een dergelijke verandering in levenswijze laten zien. Oorspronkelijk worden brandganzen gezien als specialist van hoog-Arctische broedgebieden, maar inmiddels broeden brandganzen ook in het Baltisch gebied en in de Hollandse Delta, het oorspronkelijke overwinteringsgebied. Met deze zuidwaartse uitbreiding van het broedgebied is een verandering in levenswijze gepaard gegaan: Arctisch broedende ganzen blijven migreren, terwijl Baltische broedvogels hun migratie hebben ingekort en Nederlandse broedvogels zelfs zijn gestopt met migreren.

In deze thesis heb ik de voor- en nadelen van migratie naar het noordpoolgebied onderzocht door trekkende, Arctisch broedende brandganzen te vergelijken met de niet-trekkende brandganzen die in de gematigde gebieden broeden. Daarnaast heb ik de verschillen in activiteit tussen trekkende en niet-trekkende ganzen bestudeerd om inzicht te krijgen in de gedragsaanpassingen die gepaard gaan met een migrerende levenswijze.

In het eerste deel van deze thesis heb ik mij gericht op de levensstadia die plaatsvinden in het broedgebied: reproductie en rui. De beslissing om te gaan broeden kan van groot belang zijn voor het broedsucces van de populatie. Wanneer weinig vogels gaan broeden zal het aantal jongen namelijk laag zijn. In **Hoofdstuk 2** heb ik met behulp van zendergegevens onderzocht of er verschillen zijn in de broedzekerheid van brandganzen in relatie tot de breedtegraad van het broedgebied en de start van het voorjaar. De start van het voorjaar (toename in voorjaarstemperatuur en sneeuwsmelt) bepaalt namelijk in grote mate de voedselbeschikbaarheid voor ganzen, doordat het gras wat de ganzen eten dan gaat groeien. Hoe noordelijker de ganzen broedden hoe sterker ze afhankelijk bleken te zijn van de start van het voorjaar. In jaren waarin het voorjaar vroeg was, bleek de broedzekerheid hoog te zijn, maar in jaren met een laat voorjaar was de broedzekerheid erg laag en broedden er vrijwel geen ganzen. Dit effect was afwezig voor de ganzen die broedden op de gematigde breedtegraden. De hoge broedzekerheid in het poolgebied met vroege voorjaren komt mogelijk door de grotere beschikbaarheid van nestlocaties en door de lokale beschikbaarheid van voedsel voor de volwassen ganzen. Die hebben daardoor de gelegenheid om reserves op te bouwen voor het leggen van eieren en voor het broeden. De ganzen in gematigde gebieden zijn waarschijnlijk minder afhankelijk van de start van het voorjaar, omdat het huidige agrarisch landgebruik de niet-migrerende ganzen vrijwel het gehele jaar geschikt voedsel biedt. De broedzekerheid was dan ook hoog. Het voedsel in de broedgebieden is echter ook van groot belang voor de kuikens, die vegetatie met een hoog eiwitgehalte nodig hebben om te groeien. In **Hoofdstuk 3** heb ik de groeisnelheden van kuikens in het poolgebied (Rusland) vergeleken met de kuikens in twee populatie die broeden in de gematigde zone: op Gotland (Zweden) en in de Hollandse Delta (Nederland). De kuikens in het poolgebied groeiden het snelst, gevolgd door de kuikens op Gotland en de kuikens in Nederland. De verschillen in groeisnelheid konden grotendeels worden verklaard door de verschillen in daglicht die de kuikens ervaarden. Het is daarmee waarschijnlijk dat het vooral de beschikbare foerageertijd is die de groei van de kuikens in Nederland en Zweden beperkt. De kuikens in Nederland en Zweden kunnen langzamer groeien omdat ze niet dezelfde tijdsdruk ervaren als de kuikens in het poolgebied. In het poolgebied moeten kuikens namelijk op tijd volgroeid zijn om zich voor te kunnen bereiden op de najaarstrek. Ook de volwassen vogels ervaren deze tijdsdruk in het poolgebied: broeden en de rui moeten op tijd worden voltooid om te kunnen opvetten voor de najaarstrek. In **Hoofdstuk 4** wordt de relatie tussen de timing van broeden en rui van ganzen in het Russische poolgebied vergeleken met ganzen op Gotland en in de Hollandse Delta. Over het algemeen bleken later broedende vogels later te ruien, waarschijnlijk om overlap tussen broeden en rui te voorkomen. Dit was met name zo in het poolgebied, waar de periode tussen broeden en rui het kortst was. In vrouwtjes bleek de timing van broeden en rui daarnaast sterker gekoppeld dan in mannetjes en in het poolgebied leek de periode tussen broeden en rui voor vrouwtjes te stabiliseren rond een minimum van 18 dagen. De vrouwtjes zijn verantwoordelijk voor het incuberen van de eieren, een periode waarin ze een aanzienlijk deel van haar lichaamsgewicht verliest en ook de rui kost vervolgens energie. Doordat twee energetisch kostbare periodes kort op elkaar volgen, hebben de vrouwtjes vermoedelijk tijd nodig om bij te komen van het broeden voordat ze kunnen ruien. Het is mogelijk dat dit ervoor zorgt dat vrouwtjes minder gemakkelijk de timing van broeden en rui kunnen aanpassen dan mannetjes, iets wat een belangrijke rol kan spelen bij dispersie en het aanpassen aan een nieuw broedgebied.

In het tweede deel van deze thesis heb ik mij gericht op de gedragsaanpassingen van brandganzen die gepaard gaan met migratie naar het poolgebied. Een van de grootste voordelen van de trek naar het noorden is de toenemende daglengte. Om hiervan gebruik te kunnen maken moeten ganzen wel hun dag-nacht ritme aanpassen. In **Hoofdstuk 5** wordt door gebruik te maken van lichaams-temperatuurloggers aangetoond dat ganzen bijzonder snel hun dag-nacht ritme aanpassen aan veranderende lichtomstandigheden. Hierdoor kunnen de ganzen vrijwel direct gebruik maken van de extra foerageertijd die de noordwaartse migratie biedt, zodat ze mogelijk gemakkelijker de energetische kosten van de migratie kunnen dragen. In **Hoofdstuk 6** laat ik aan de hand van versnellingsmetergegevens zien dat de migrerende ganzen over het gehele jaar actiever zijn dan niet-migrerende ganzen. Dit komt waarschijnlijk doordat ze meer moeten foerageren vanwege de energetische kosten van migratie. Waar de toenemende hoeveelheid daglicht in het voorjaar, tezamen met de noordwaartse migratie, een hogere foerageeractiviteit voorafgaand aan de voorjaarstrek faciliteert, moeten de Arctische ganzen in het najaar juist onder afnemende licht- en voedselcondities reserves opbouwen voor de najaarstrek. De trekkende ganzen zijn daardoor voor een langere periode actief buiten de daglichtperiode ('s nachts) dan de niet-trekkende ganzen. Hieruit concluderen we dat een migrerende levenswijze extra energetische kosten met zich meebrengt, met bovendien tijdsdruk om deze kosten te compenseren.

Uiteindelijk kunnen we concluderen dat zowel een migrerende als niet-migrerende levenswijze voor brandganzen momenteel levensvatbaar is. Hoewel er duidelijk kosten zijn verbonden aan de migratie naar het poolgebied in de vorm van energie en tijd, biedt het broeden in het poolgebied ook de condities om hiermee om te gaan. De uitbreiding van het broedgebied van de brandgans is op zichzelf een opzienbarende ontwikkeling. Het zijn hoogstwaarschijnlijk door de mens veroorzaakte veranderingen geweest (verhoogde voedsel kwaliteit door bemesting en verlaagde predatiedruk door vervolging van roofdieren) die het voor brandganzen mogelijk hebben gemaakt te broeden op lagere breedtegraden (**Hoofdstuk 7**). De balans tussen de voor- en nadelen van migratie kan dus veranderen wanneer er veranderingen optreden in de leefomgeving van trekvogels. Daarmee kunnen ook veranderingen in levenswijze optreden, waaronder het stoppen met migreren. Tegenwoordig hebben mensen een grote invloed op het wereldwijde landgebruik en het klimaat. De impact van de mens op de leefomgeving van trekvogels zal dan ook bepalend zijn voor de toekomst van de migrerende levenswijze van veel vogels.

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