Revolutionary non-migratory migrants

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Wild caught barnacle geese near Tobseda, Russia

Chapter 1

General Introduction

Rudy M. Jonker

-There is no greater anomaly in nature than a bird that cannot fly-
Charles Darwin, Origin of Species – 1859

And yet we know that there are birds that cannot fly and seem to function perfectly without the ability to fly. Similarly, one could say that there is no greater anomaly in migration ecology than a migratory bird that does not migrate. And yet we know an example of such a migratory bird that does not migrate.

But to fully grasp and appreciate the concept of such a revolutionary non-migratory migratory bird and to appreciate and understand the logic and motivation for this thesis let me introduce the concept of migration first. With migration I mean the behaviour by which individuals seasonally migrate between two distant locations, and where reproduction only occurs in one of these locations (Dingle and Drake 2007). Migratory birds make use of the fact that some areas are a better environment for them during some part of the year and other areas during the other part of the year. For example, many migratory birds migrate to the arctic in summer. They benefit from the long days, the consequent opportunities for foraging (reviewed in Alerstam et al. 2003) and the relative safety (McKinnon et al. 2010). However, at some moment in autumn the conditions become too harsh in the arctic to stay there and they travel southward again.

How do they know where to go and when to go there? In order to migrate successfully, birds have to arrive at their breeding area at the right time. A bird ideally arrives at its breeding area at the moment that gives the individual the best chances for successfully raising offspring. And it ideally leaves that area at the moment that gives the individual the best chances to keep its offspring alive and to stay alive itself, in order to breed again next year. For many migratory birds these decisions are regulated by their genetic programming (Berthold and Querner 1981). Triggered by stimuli such as day length, they get in the migratory mood and follow cues such as magnetic fields (reviewed in Alerstam et al. 2003) to orientate and successfully reach their destination. If the result of their rules is arrival at a safe place to ensure their own survival, with good opportunities for raising offspring successfully, then these individuals will outcompete individuals with suboptimal programming. However, natural selection will select those individuals that fit their environment best. So, when the environment is stable, having migration behaviour genetically inherited is a good mechanism. But when the environment changes suddenly or frequently, the adaptation to the new circumstances is relatively slow.

A well-studied example of a case where a bird species' response to changing environment is studied, is the Pied Flycatcher *Fycedula hypoleuca*. Pied flycatchers breed in the Netherlands at the moment that, when the eggs hatch, the availability of food is maximal. To arrive in the Netherlands on time, they depart from their wintering grounds in

Africa on time. The pied flycatchers then arrive just a few days prior to their preferred breeding date, to allow themselves some flexibility to adjust to the normal variation in temperatures in the Netherlands, as the peak of food advances with increasing temperatures and vice versa. Over the past 30 years, however, the spring temperatures have increased to such an extent that the optimal timing of breeding is before the pied flycatchers arrive in the Netherlands, which is suggested to be constraint by the departure date from their African breeding grounds (Both and Visser 2001). Because this departure date is triggered by local conditions, which have changed at a different rate than the conditions in the Netherlands, they do not advance their arrival in the Netherlands as much as would be optimal form the perspective of matching the hatching of offspring with the food peak. Consequently, the populations of pied flycatchers in the Netherlands have declined by about 90% (Both et al. 2006). If this departure date from Africa is triggered by day length (which is obviously not changing with increased temperatures), and if this day length threshold for departure is inherited genetically, the rate of adaptation is limited by the amount of existing variation or mutation rates.

There is another way of inheriting migratory decisions, which is by means of cultural transmission. Species such as geese, cranes, swans and storks learn migratory behaviour from parents and have very strong parent-offspring associations (Owen 1980). Strikingly, in a review on flexibility and constraints in migratory systems, Sutherland (1998) showed that species with extended parental care and culturally inherited migration (in contrast to short parental care and genetically inherited migration) adjusted their migratory routes best to changing conditions. With an extended period of parental care I mean that the parents provide care to the offspring until long after nutritional independence. However, this strong parent-offspring association and consequent natal philopatry (offspring having a preference to stay in the same colony or breeding location as the parents) also result in strong conservatism. So, if the parents have a certain migratory routine, and their offspring copies that, and their offspring copies that, and so on, the migratory behaviour will remain the same, unless this transmission between parents and offspring is unsuccessful. The potential result of this conservatism is that the traditional migratory behaviour exhibited is not necessarily the optimal behaviour for the current circumstances (Corten 2002). But apparently, traditions are still more flexible than genes.

Geese thus have extended parental care, and culturally inherited migratory behaviour. A very well studied goose species is the Barnacle Goose *Branta leucopsis*. An interesting aspect of barnacle geese is that they have shown many changes in their migratory be-

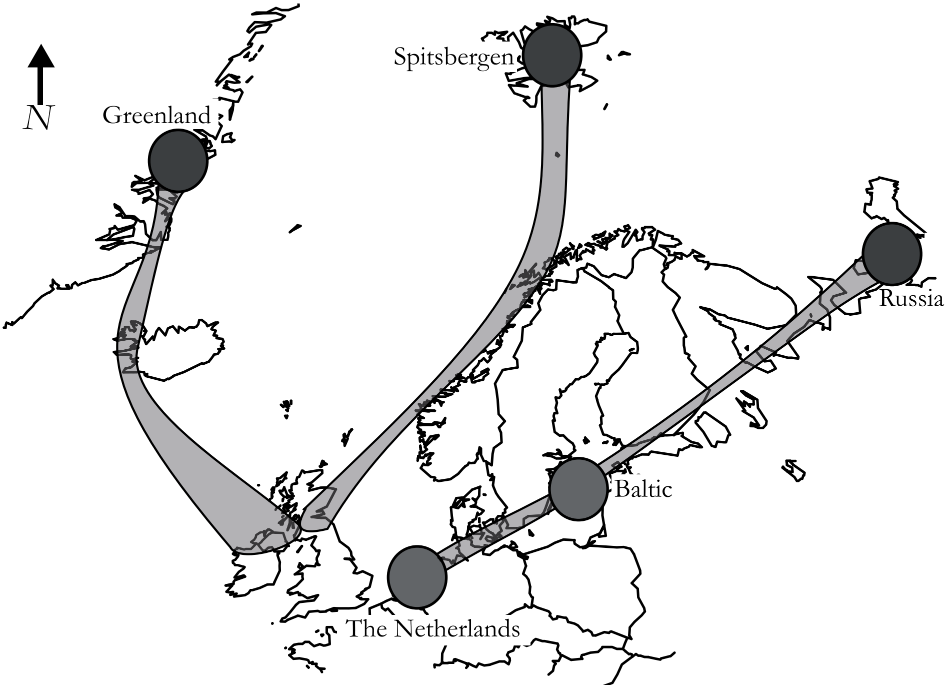

Figure 1.1. Schematic map of barnacle goose populations.

haviour since the 1970s.

Before the 1970s, there were three major populations of barnacle geese, characterized by different flyways (Figure 1.1). The Greenland population breeds on the east coast of Greenland. They migrate southward in autumn via a stopover on Iceland to their wintering area in Ireland and the west coast of Scotland. In spring, they migrate, again via a stopover on Iceland, back to Greenland to breed again (Ogilvie et al. 1999). The Spitsbergen population breeds on coasts on Spitsbergen and migrate in autumn via a stopover in Norway to their wintering area in Scotland and England. In spring they migrate again via a stopover in Norway to breed on Spitsbergen (Owen and Black 1999). The Russian population breeds in arctic Russia and migrates via stopover sites in the Baltic to its wintering area in the Netherlands and migrates in spring via the stopovers in the Baltic to breed in Russia (Ganter et al. 1999).

Since the 1960s all the populations of barnacle geese have increased drastically, and the global population totals now approximately 800,000 (Fox et al. 2010), with the vast majority (approximately 700,000) breeding in the Russian arctic. In contrast to this, in the 1960s the Russian population consisted only of 25,000 individuals (Ganter et al. 1999) and the status in those days was nicely illustrated by Johnsgard (1978):

"All of these figures would suggest a total world population of about 50,000 barnacle geese, making this species one of the rarer forms of true geese (Kumari, 1971). This, added to the seemingly low

reproductive efficiency of barnacle geese, makes them vulnerable to rapid population declines in spite of apparent recent increases."

However, in addition to the population increase, also the migratory behaviour of the Russian breeding barnacle geese has changed since the 1970s. It are these changes that form the prime focus of this thesis. The first change is that the commencement of spring migration, which used to take place around half April, has delayed with approximately one month (Eichhorn et al. 2006; Eichhorn et al. 2008). The timing of spring migration is suggested to be extremely important for successful breeding. Because geese are capital breeders, which means that they use resources for breeding that have not been acquired locally, they have to bring resources for breeding to the breeding site in the form of fat. Geese migrating most efficiently will thus arrive with most fat, and breed best (Drent and Daan 1980; but see Klaassen et al. 2006a). To do so, geese follow a green wave of fresh plant growth during spring migration. By being at a location where the conditions for nutritious grass growth are optimal during each moment in spring, geese maximize the amount of energy stored per unit of time. However, an individual goose first has to arrive at the breeding site, i.e., it has to stay alive. To avoid predation, geese spend time on being vigilant, and to minimize the time spent on vigilance, the so-called landscape of fear plays a role (Brown 1988; Pomeroy et al. 2006). Safer locations will allow an individual to forage more, while dangerous locations (which can be very profitable!) require more vigilance. These two drivers, safety and energy will thus shape the optimal location and foraging behaviour at each stage of spring migration (Alerstam and Lindström 1990, but see propositions). An extra challenge then is that arriving in the Arctic too early is not really a smart move because the Arctic conditions will be quite hostile prior to the onset of spring and require burning fat to stay alive. Fat that was imported to the Arctic by the individual goose and could have been used much better during breeding. But arriving too late causes breeding to start too late, and offspring to hatch at a suboptimal timing (Prop et al. 2003). And because the Arctic summer is short, not a day can be wasted by not being there on time.

So, the question arises what suddenly has changed the timing of spring migration in Russian breeding barnacle geese. Has the moment of peak plant growth changed as a result of climate change? Have the food conditions changed because of the increasing population? Or has it become more dangerous during migration? These questions will all be addressed in chapter two.

Revisiting the mentioned mechanism of culturally inherited migration, the consequences of this delay in migration suddenly become very interesting. We do know that geese take care of their offspring for almost a year (Mayr 1942; Hochbaum 1955; Baker 1978;

Owen 1980), or at least well into spring migration (Black and Owen 1989). During migration, parents with offspring face the trade-off between spending time on parental care, by being extra vigilant and help offspring compete for food (Scott 1980), and spending time on foraging to increase the chances of success of the next breeding attempt. Parental care is terminated when the reward of the extra investment in the current offspring (being extra vigilant for offspring, helping compete offspring with other families, allowing offspring to forage in the same patch as yourself) becomes smaller than the reward of investment in future offspring (storing fat, staying alive) (Trivers 1972). But the offspring will disagree with this termination, as long as the reward of being taken care of for a longer time, exceeds the cost to its parents fitness times 0.5, because offspring has on average a relatedness of 0.5, and will thus care twice as much about his own fitness than of the parent. This parent-offspring conflict (Trivers 1974) leads to an increase of attacks by parental barnacle geese during migration, followed by a sort of greeting by the offspring. Eventually, parental care is terminated, as is nicely described by Black and Owen (1989). The close association between parents and offspring during migration allows successful transmission of migratory behaviour. So, when the commencement of spring migration is delayed, do barnacle geese also adjust the timing of termination of parental care? I answer this question in chapter three.

The most striking migratory change however, is that some Russian barnacle geese became non-migratory. After a breeding population first emerged on Gotland, Sweden, in the 1970s, which still migrated but only half the distance (Larsson et al. 1988), barnacle geese started breeding in the Netherlands (Meininger and Van Swelm 1994), and are very successful (Ouweneel 2001). This population does not migrate and stays in the Netherlands throughout the year. Their main breeding locations are in the south of the Netherlands in the Dutch delta.

So, we have non-migratory barnacle geese in the Netherlands. A number of differences between the migratory and non-migratory life style can be identified. First of all, migration is a risky business. Not only do geese encounter many predators along the migratory route that are hardly present in the Netherlands, such as white-tailed eagles *Haliaeetus albicilla*, also uncertain weather conditions (Newton 2007) and uncertain food conditions (Bauer et al. 2006) make it an enterprise that has quite some risk of failure. It has been shown for another migratory bird, the Black-throated Blue Warbler *Dendroica caerulescens*, that the mortality rate during period of migration is fifteen times higher than during non-migratory periods. And also for the Barnacle Goose it has been shown that the juvenile survival after fledging is almost twice as high for non-migratory than migratory barnacle geese (Van der Jeugd et al. 2009). Such a difference in expectations of the future give rise to questions on what is the best parental investment strategy (Clutton-Brock 1991; Forbes 2009). It is expected that for individuals with high expected future reproductive success, lower levels of parental investment are optimal, as there is much to lose. In contrast, for individuals with low expected future reproductive success higher levels of investment are optimal (Pianka 1976; Stearns 1976). Chapter four thus answers the question what the consequence is of a change from a migratory to a non-migratory life-style for the duration of parental care in barnacle geese.

An important question for the emergence of this non-migratory population is where it comes from. It is probably no coincidence that shortly after completion of the Delta works, and thus the lower chances of nests built close to the water being flooded, the colonization of the Netherlands as a breeding area started. But from where did these individuals come? And has this population grown by its own reproduction or were individuals recruited from other populations? To answer all these questions, genetic analyses are a very useful tool (Wink 2006). Genetics allows us to trace how events in the past took place, because different sorts of events leave different genetic patterns. To study this for the Barnacle Goose markers were needed. Migratory birds are difficult to study with population genetics, and differentiation between populations requires high statistical power because of the mobility of the individuals. Earlier attempts to study goose (Branta) genetics using microsatellites failed (Loonen & Burke pers. comm.). Single Nucleotide Polymorphisms (SNP) are markers that provide us with the statistical power to study this in detail (Morin et al. 2004). Therefore, we designed a whole new set of 384 SNP markers which is presented in chapter five. In chapter six, I use this SNP set to study the population genetics of the Barnacle Goose, to find out how and by whom the colonization of the non-migratory population in the Netherlands occurred.

By using the migration system of the Barnacle Goose I will provide a case study of how migratory changes can occur, what their adaptive value is and how they can be understood. A major consequence of these changes in migration is that the amount of goose damage in the Netherlands drastically increased (Faunafonds 2009). A delay in migration causes migratory barnacle geese to extend their stay into the start of the growing season in agriculture, and as non-migratory geese stay in the Netherlands year round, the damage increases even more. However, these consequences distract from the amazing revolutionary change in behaviour and I hope this thesis will not only increase the insights we have in migratory changes in general and in barnacle geese specifically, but also increase the appreciation for our revolutionary non-migratory migrants.

Wooden sculptures of eagle and goose in Kiideva, Estonia

Chapter 2

Predation danger can explain changes in timing of migration

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Abstract

Understanding stopover decisions of long-distance migratory birds is crucial for conservation and management of these species along their migratory flyway. Recently, an increasing number of barnacle geese breeding in the Russian Arctic have delayed their departure from their wintering site in the Netherlands by approximately one month and have reduced their staging duration at stopover sites in the Baltic accordingly. Consequently, this extended stay increases agricultural damage in the Netherlands. Using a dynamic state variable approach we explored three hypotheses about the underlying causes of these changes in migratory behaviour, possibly related to changes in (i) onset of spring, (ii) potential intake rates and (iii) predation danger at wintering and stopover sites. Our simulations showed that the observed advance in onset of spring contradicts the observed delay of departure, whereas both increased predation danger and decreased intake rates in the Baltic can explain the delay. Decreased intake rates are expected as a result of increased competition for food in the growing Barnacle Goose population. However, the effect of predation danger in the model was particularly strong, and we hypothesize that barnacle geese avoid Baltic stopover sites as a response to the rapidly increasing number of avian predators in the area. Therefore, danger should be considered as an important factor influencing migratory behaviour of geese, and receive more attention in empirical studies.

Introduction

In migratory species, flexibility allows dealing with a continuously changing environment. Illustratively, Sutherland (1998) presented an overview of bird species that showed flexibility in their migratory behaviour to changing environmental conditions. He described changes in the use of wintering, breeding and staging areas, occurring in a wide range of families. Recently, Jonzén et al. (2006) suggested a climate-driven evolutionary change in the timing of spring migration for a number of long-distance passerine migrants (Jonzén et al. 2006, but see Both 2007). Changes in migration can also be caused by factors other than climate. Gill et al. (2001) for example, showed that an increasing population of Black-tailed Godwits *Limosa limosa islandica*, wintering in the UK, established new wintering sites on less suitable sites than the original wintering sites. They suggested that the carrying capacity of the original sites was reached, forcing the Black-tailed Godwits to winter elsewhere. Additionally, Klaassen et al. (2006b) adopted a dynamic state variable model and showed that pink-footed geese *Anser brachyrhynchus* respond to scaring practices by farmers in Norway by changing their use of stopover sites. Alerstam & Lindström (1990) discussed minimization of time, energy and predation during migration as the main drivers of evolution in migratory behaviour. The aforementioned examples of migratory change might represent responses to changes in one or more of these factors. Identifying possible causes of these changes, is essential for understanding flexibility in migratory behaviour.

Since the early 1990s, an increasing number of barnacle geese *Branta leucopsis* breeding in the Russian Arctic have delayed their departure from their wintering site in the Netherlands by approximately one month. The geese reduced their staging duration in the next stopover area in the Baltic (traditionally used by the entire population) according to the delayed departure from the Netherlands, such that some migrants virtually skip the Baltic stopover site altogether (Eichhorn et al. 2006; Eichhorn et al. 2009). Because of these changes, the question arose what has caused the delayed departure from the wintering site and decreased use of the Baltic stopover site. Compared to changes in (migration) phenology in other bird species (Marra et al. 2005; Stervander et al. 2005; Visser and Both 2005; Jonzén et al. 2006), the rate of change of approximately 3 days/year as observed in the Barnacle Goose is unprecedentedly large. One important consequence of the delayed migration of barnacle geese is an increased agricultural damage in the Netherlands of approximately €350,000 annually, and this figure is growing rapidly (Faunafonds 2009). Successful management actions require the identification of factors and processes affecting departure and staging decisions. Therefore, we have formulated three possible explanations for the delay: barnacle geese have delayed their departure as a consequence of changes in (i) onset of spring, (ii) potential food intake rates, and (iii) predation danger (Lank and Ydenberg 2003).

(i) *Advanced onset of spring*

Recently, several studies have found that migratory birds responded to climate-driven changes in plant phenology with advanced laying dates (Crick et al. 1997), advanced spring arrival dates (Stervander et al. 2005; Jonzén et al. 2006; Gordo 2007) or increased rate of spring migration (Marra et al. 2005). Climate change could result in higher spring temperatures in some regions, leading to earlier growth of the vegetation. Barnacle geese are thought to schedule their migration according to the "green wave" of fresh plant growth along the flyway (Van der Graaf et al. 2006b). However, this relationship might not be that straightforward, because geese may prioritize other factors, such as safety or food quality. Therefore, the potential effect of onset of spring is investigated in this study.

(ii) *Decreased intake rate*

The potential intake rate at a stopover site, i.e. the intake per day a goose can gain if foraging at maximum intensity, limits the rate at which geese can replenish their energy reserves (Beekman et al. 2002). Earlier studies have shown that decreased availability and reduced quality of food can make a stopover site less attractive (Van der Graaf et al. 2007). Van der Graaf (2006) reported lower intake rates in the Baltic as compared to the Netherlands. Moreover, as the total number of barnacle geese passing through the Baltic has increased drastically over the past thirty years (Van der Jeugd et al. 2009), the competition for food at the Baltic stopover site may also have intensified (Forslund and Larsson 1991). Additionally, desertion of farmland, and thus reduced facilitation by cattle grazing, in these regions may also have decreased intake rates (Prins and Gordon 2008). For these reasons, decreased potential intake rates at the Baltic stopover site may cause barnacle geese to reduce staging time or even completely skip this site. Then, the geese could fly directly to one of the next stopover sites in Russia; however, since food there becomes available only later in spring, they have to delay their departure from the Netherlands until spring starts in the arctic stopover sites in Russia.

(iii) *Increased predation danger*

Increased predation danger can reduce the attractiveness of a site because of its lethal and non-lethal effects (Ydenberg and Dill 1986; Cresswell 2008). Although safety has long been acknowledged as potentially important for successful migration (Alerstam and Lindström 1990), it has received little attention so far and the few studies on the impact of predation danger on migration have not led to unambiguous conclusions (Alerstam et al. 2003; Ydenberg et al. 2007). While a number of studies indeed demonstrated the effects of predators on body mass, stopover duration and site usage (Lank et al. 2003; Pomeroy 2006), some of the results are difficult to interpret (Fransson and Weber 1997), and others even deny at least some of the suggested effects of predation danger (Dierschke 2003).

In this study, we used a dynamic state variable model to analyze whether these three hypotheses can explain the observed changes in migratory behaviour of Barnacle geese.

Methods

We used a dynamic state variable model to predict the migration strategy of the Barnacle Goose that maximizes expected lifetime reproductive success under different environmental circumstances. This type of model is most suitable as it includes future goals (maximising long term reproductive success) when defining decisions that lead to achieving these goals (Houston and McNamara 1999; Clark and Mangel 2000). We used an existing model (see for more details Weber et al. ; Klaassen et al. 2006b; Bauer et al. 2008) which we parameterized for the Barnacle Goose. We shortly explain the model here to give insight in the logic of the parameters used and to facilitate understanding our predictions.

The dynamic state variable model

The state of the goose in the model was characterized by its energy stores x and its location i. At each time step of one day, t=0,1…T, the state of body reserves was calculated, and according to state, location and time decisions for optimal migration were made. For computational reasons, x took only integer values between 0 and x_{max}=100. One unit of x was equivalent to 232 kJ, representing 1% of the caloric value of the maximum body reserves (see Table 2.1 for an overview of parameters). If the body reserves fell to zero, the goose died of starvation. We considered 4 different locations: a wintering site in the Netherlands, stopover sites in the Baltic sea region and at the Kanin peninsula in Russia, and a breeding site N at the Barents Sea coast in Russia (Van der Jeugd et al. 2003) (Figure 2.1). Breeding was only possible at the breeding site. At t=0 (March 1) the goose started at the wintering site and simulations ended when it reached the breeding site or when t reached T, a predefined endpoint which was set to t=121 (June 29), approximately 3 weeks after the optimal time window for breeding. The expected reproductive success of the goose, with body reserves x at time t at location i, was denoted by $F(x,t,i)$.

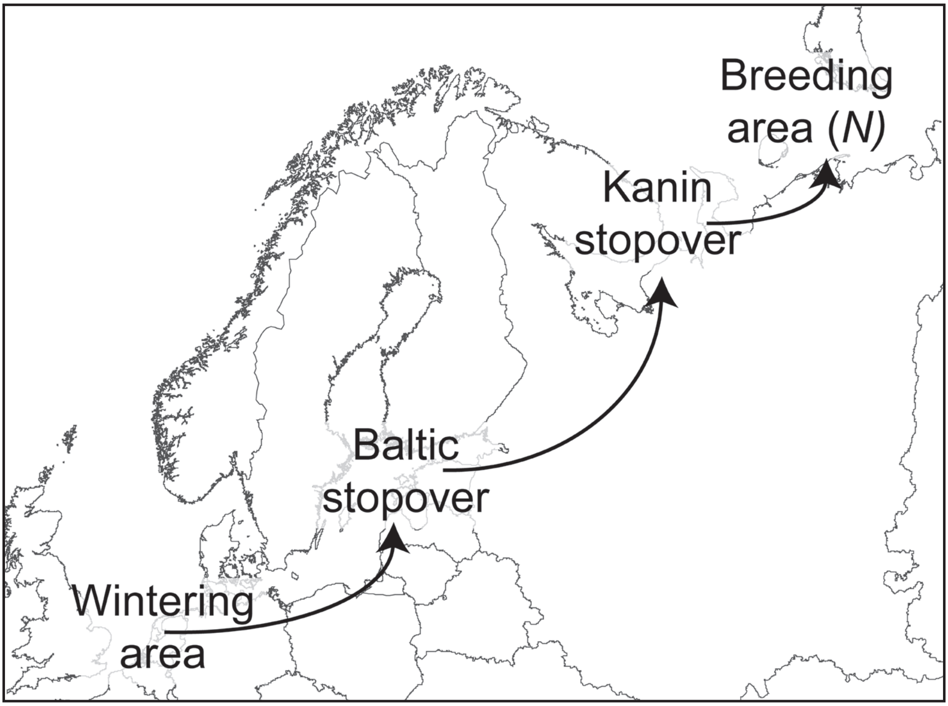

Figure 2.1. Migration route of Russian barnacle geese.
A schematic overview of the flyway of the Russian population of the Barnacle Goose. In spring (April-May), barnacle geese depart from The Netherlands to stopover areas in the Baltic. After a stop of a few days to a few weeks they depart to pre-breeding areas in Northern Russia. The geese arrive at their arctic breeding grounds early June and start breeding immediately.

Terminal reward function

The terminal reward was defined as the reward at T, and served as a starting point for the backward iteration. Upon arrival at the breeding site N the expected reproductive success $F(x,t,N)$ depended on the body stores at arrival as well as the timing of arrival (Prop et al. 2003). Additionally, a component was added for expected future reproductive success B_T because Barnacle geese are long-lived animals with many years of breeding attempts. Thus:

$$F(x,t,N) = K(t) \cdot K(x) + B_T \qquad eqn.\ 2.1$$

where $K(t)$ was the function of the timing of arrival, $K(x)$ the function of the body stores on arrival, and B_T was set to 2, representing the expected future reproductive success given that an individual actually survived at any site until T. Both $K(t)$ and $K(x)$ result in 0 reward if an individual had not arrived at breeding site N at T. Subsequently, the effect of timing of arrival was incorporated by a step function, meaning that breeding was only possible if arriving at the breeding grounds within the set time-limits:

$$K(t) = \begin{cases} 0 \text{ if } t < June\ 6 \text{ or } t > June\ 11 \\ 1 \text{ if } June\ 6 \leq t \leq June\ 11 \end{cases} \qquad eqn.\ 2.2$$

(Prop et al. 2003; Van der Jeugd et al. 2009). The effect of body reserves on breeding success was described by a sigmoidal shape function based on data from the Pink-footed Goose (Prop et al. 2003), indicating that the chance of successful breeding increased if body stores upon arrival at the breeding site exceeded a certain threshold x_c. We assumed a similar relationship for barnacle geese. Thus:

$$K(x) = \frac{1}{2}\left(\frac{e^{w(x-x_c)} - e^{-w(x-x_c)}}{e^{w(x-x_c)} + e^{-w(x-x_c)}} + 1\right) \qquad eqn.\ 2.3$$

where the shape parameter w was set to 0.028 and x_c, the threshold for successful breeding, was set to 15080 kJ ($x_c = 65$)

Backward iteration

At each time step a goose decided whether to stay at its present location and forage, or to depart to another location. When staying at location i, the potential intake rate (defined as metabolizable energy intake according to Bruinzeel et al. (1997) of the goose was site- and time-dependent and had predefined stochasticity [$g(i,t)$, kJ day-1]. However, the actual intake rate depended on the foraging intensity u, ranging from 0 (no foraging) to 1 (continuous foraging). The actual intake rate minus the energy expenditure e [kJ day-1] resulted in the energy available for the storage of reserves. However, foraging with a particular intensity and storing reserves had a cost in terms of predation risk, defined by $\beta(x,u)$:

$$\beta(x,u) = m_{\beta(i)} \frac{(x + ug(i,t) - e)^{a+1} - x^{a+1}}{(a+1)(ug(i,t) - e)} \qquad eqn.\ 2.4$$

where a, the mass-dependent escape performance exponent, was set to 2 and the site-specific constant attack rate (Weber et al. 1998) $m_{\beta(i)}$ is set to 10^{-8}. The parameter $m_{\beta(i)}$ is the predation danger according to the definition by (Lank and Ydenberg 2003). Thus, the goose foraged with the intensity that maximized its expected reproductive success F:

$$H_f(x,t,i) = \max_u \left[(1 - \beta(x,u)) F(x + ug(i,t) - e, t+1, i) \right] \qquad eqn.\ 2.5$$

Alternatively, when departing to another site j, the goose chose the site j that maximized F:

$$H_d(x,t,i) = \max_j \left[F\left(x_a, t + \left(\sum_{z=i}^{j-1} D_z / v \right), j \right) \right] \qquad eqn.\ 2.6$$

This choice depended on the distance between the sites [D_z (km)], the speed of flight [v (km day-1)], and the reserves upon arrival (X_a) at site j. The latter was defined by

$$X_a = \left(\frac{c^2}{(c - (c(1 - (1 + x/x_{\max})^{-0.5}) - D))^2} \right) \cdot x_{\max} \qquad eqn.\ 2.7$$

where D was the distance covered. The constant c in this equation was defined by

$$c = \frac{D_{\max}}{1 - (1 + x_f/x_{\max})^{-0.5}} \qquad eqn.\ 2.8$$

where x_f was the level of body reserves available for flight, which equaled x_{max} for barnacle geese, and D_{max} was the maximum flight distance defined by

$$D_{\max} = \frac{x_{\max}}{f} \qquad eqn.\ 2.9$$

where f was the average flight cost [kJ km-1] (Nolet et al. 1992; Butler et al. 2000; Ward et al. 2002). To find the fitness-maximizing decision, we calculated the fitness consequences of the behavioural alternatives, i.e., to forage or depart, for all combinations of state, location and time and chose the one with the highest fitness. The thus obtained optimal decision matrix showed the best decision for each time step and for all possible levels of body reserves and sites, namely:

$$F(x,t,i) = \max\left[H_f(x,t,i), H_d(x,t,i) \right] \qquad eqn.\ 2.10$$

Table 2.1. Parameterization of the model.

Parameter		*unit*	*Reference*
Model parameters Barnacle Goose			
Lean body mass	1500	g	Eichhorn 2008
Maximum body mass	2300	g	Eichhorn 2008
Potential mass reserves	800	g	
Energy density	29	kJ/g	(Madsen and Klaassen 2006)
Total energy reserves x_{max}	23.2	MJ	
Energy density per x	232	kJ	
Flight speed v	18	m/s	(Green 2001)
Average flight costs f	6.23	kJ/km	(Nolet et al. 1992; Butler et al. 2000; Ward et al. 2002)
Daily energy expenditure e	4.7	kJ	(Bruinzeel et al. 1997)
Model parameters of the staging areas of the Russian flyway			
Wintering site The Netherlands			
Distance to wintering site	0	km	
Maximum metabolizable energy intake g	1397	kJ/day	Eichhorn 2008
Stop-over site Baltic			
Distance to wintering site	1270	km	
Maximum metabolizable energy intake g	1939	kJ/day	Eichhorn 2008
Peak date of food availability	May 14		(Van der Graaf et al. 2006b)
Stop-over site Kanin			
Distance to wintering site	2910	km	
Maximum metabolizable energy intake g	2296	kJ/day	Eichhorn 2008
Peak date of food availability	May 20		
Breeding site Kolokolkova Bay			(Van der Jeugd et al. 2003)
Distance to wintering site	3270	km	
Time-window of arrival for optimal arrival $K(t)$	June 5 – June 10		(Eichhorn et al. 2006)

Forward simulation

Based on the decision matrix, optimal migration was simulated for each goose. The simulations started at t=0, each goose started with a random amount of body reserves between 4640 kJ $\leq x \leq$ 11600 kJ, and ended when the bird reached the breeding site, died, or passed the time limit T at any other site. In the simulations, we assumed geese had full knowledge of the environment, i.e. the geese experienced the same conditions in the forward simulation for which the optimal decisions were calculated in the backward calculation. The actual experienced potential intake rate $g(i,t)$ for each individual was drawn from a distribution with a predefined stochasticity.

Scenarios

We analyzed the three different hypotheses by step-wisely changing the relevant model-parameters, i.e., onset of spring, intake rates and predation danger. For all scenarios, both backward iteration and forward simulations were run. First, we changed onset of spring in the Baltic staging site from 24 April to 3 June in steps of 5 days. Onset of spring was defined as the point in time when food availability $g(i,t)$ first reached its highest value. Second, we changed food availability in the wintering and Baltic stop-over site from 1392 kJ d-1 to 2784 kJ d-1 in steps of 232 kJ d-1, and in all possible combinations for both sites.

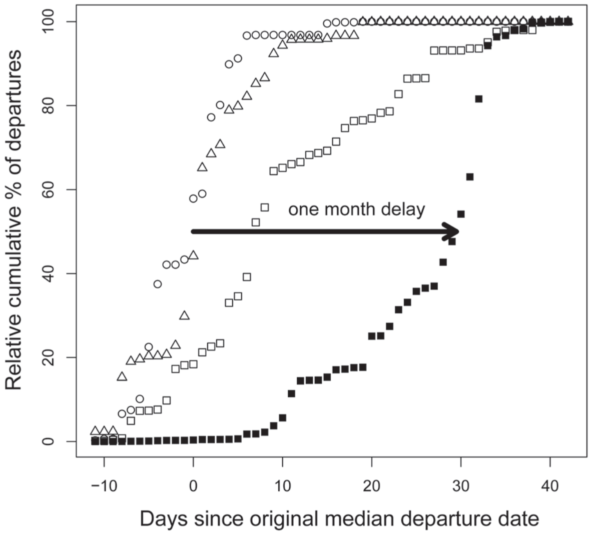

Figure 2.2. Observed delay in onset of spring migration. The departure dates from the wintering grounds in the Netherlands, shown as the relative cumulative percentage of departure as a function of days since the median departure date in the 1970s. Data points represent per day the mean relative cumulative passage count at Ottenby bird observatory over a certain period (circles: 1970-1979, triangles: 1980-1989, open squares: 1990-1999, solid squares: 2000-2004). The median departure date in the 1970s was April 12.

Third, we increased predation danger ($m_{\beta(i)}$) in the Baltic site from 10^{-10} to 10^{-6} with 16 logarithmically equal steps (10^{-10}, $10^{-9.75}$, $10^{-9.5}$, … , $10^{-6.5}$, $10^{-6.25}$, 10^{-6}). We choose this range of values based on the value of 10^{-8} used by Klaassen et al. (2006b) and the value of $2 \cdot 10^{-6}$ used by Weber et al. (1998).

We compared the model predictions of the three scenarios with passage data from the Ottenby bird observatory (56°11´45´´N, 16°23´56´´E) from 1970 until 2004 (adapted from Eichhorn et al. 2008, see Figure 2.2). Ottenby is situated on a main migratory corridor for barnacle geese traveling from the Netherlands to Baltic stopover sites (Ganter et al. 1999). Because the total population of the Barnacle Goose also greatly increased during that period, we used the relative cumulative percentage of passed dates. The most plausible predictions were those that showed a delay in departure equivalent to the observed delay of one month. All results were analyzed with *R*.2.8.1 (*R* Development Core Team, 2009).

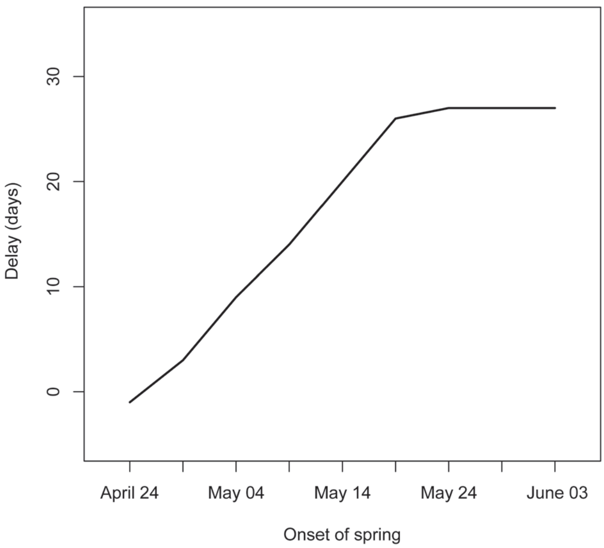

Figure 2.3. Predicted delay in onset of spring scenario. The delay in departure (in days from April 12, which was the median departure date in the 1970's) from the wintering site in the Netherlands as a function of onset of spring. In the model, the geese responded to a change in the peak date of intake rate such that they advance departures with an earlier spring and vice versa, they would depart later from the wintering site if spring in the Baltic would be delayed.

Results

Advancing the onset of spring in the Baltic by a given unit of time led to an equally advanced departure date from the wintering site for most of the range tested in our simulations (Figure 2.3). Additionally, the simulations showed that the geese always depart from the Dutch wintering site just before the onset of spring in the Baltic.

Decreasing intake rates in the Baltic stopover sites by 1392kJ/day led to a delay in departure date from the wintering site of 29 days (mid April – mid May) (Figure 2.4). If, alternatively, the intake rates in the wintering site increased, the geese delayed their departure date by only 16 days (Figure 2.4).

Increasing predation danger in the Baltic above the predation danger of the other sites led to a rapid delay of 28 days (mid April – mid May) in departure date from the wintering site (Figure 2.5). When predation danger was increased further, a growing proportion of geese stopped using the Baltic stopover site (Figure 2.6). However, a small

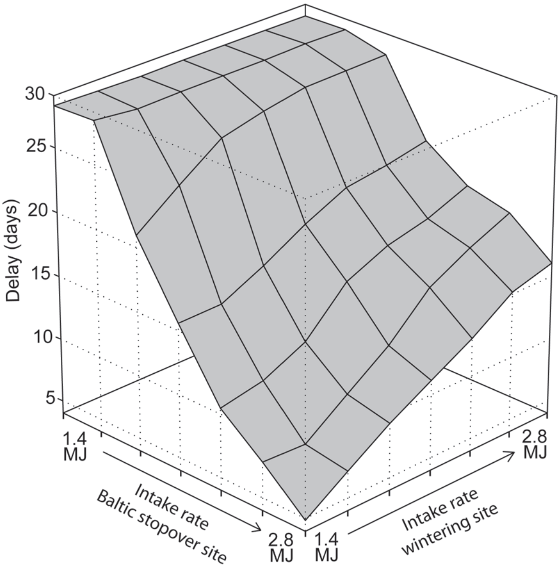

Figure 2.4. Predicted delay in intake rate scenario.
The predicted delay in departure date (in days from April 12, which was the median departure date in the 1970's) from the wintering site in the Netherlands to a changed intake rate, ranging from 1.4 MJ to 2.8 MJ, at the wintering site and the Baltic stopover site.

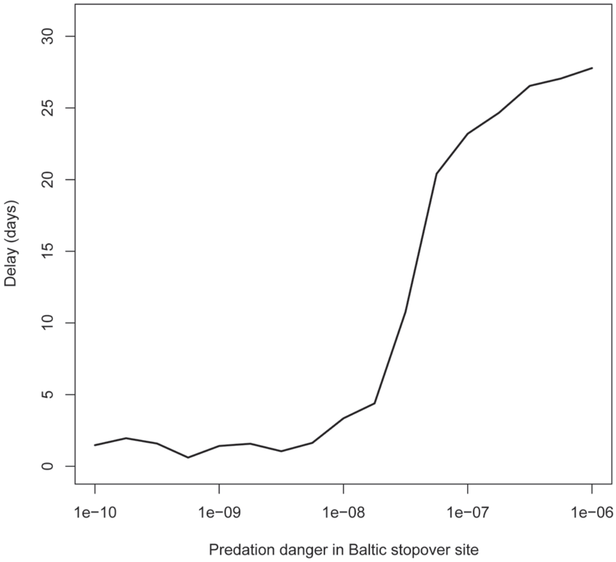

Figure 2.5. Predicted delay in danger scenario.
The delay in departure (in days from April 12, which was the median departure date in the 1970's) from the wintering site in the Netherlands as a function of predation danger at the Baltic stopover site. Above a predation danger of $3 \cdot 10^{-8}$, the geese adjusted their migration by abruptly delaying their departure date from the wintering site by up to 28 days.

proportion geese still visited the Baltic, and stayed for a few days only. They had low energy reserves, and apparently, could not skip this site as they were in dire need of replenishing their body stores.

Discussion

Our simulations showed that the delayed departure of barnacle geese from their wintering grounds by up to one month can be explained by either decreased potential intake rates or increased predation danger in the Baltic stopover site. In contrast, an advanced onset of spring fails to explain such a delay. The predicted response to an advanced spring growth is opposite to a delayed departure actually observed in the field. According to our simulations, an advancement of spring of 8 days (as predicted by Van der Graaf (2006) based on growing degree days) should advance departure by 8 days too.

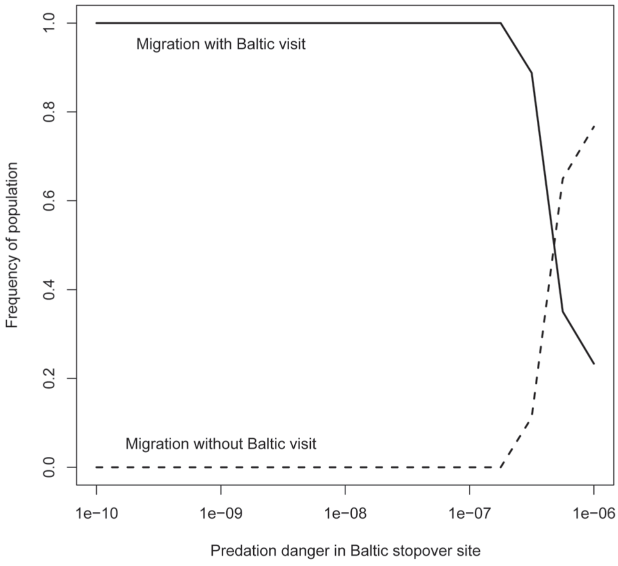

Figure 2.6. Predicted use of Baltic stopover site in danger scenario.
The predicted response to increased predation danger, described as the proportion of the geese that make use of the Baltic as a stopover site. With low predation danger all geese are predicted to use the Baltic stopover site (solid line), i.e. no skipping of the Baltic (broken line). However, with increasing predation danger the majority (+/- 75%) of the geese skip the site while some geese with (very) low body reserves continue to use the Baltic stopover site for a few days to build up extra reserves.

Interestingly, also the barnacle geese breeding on Spitsbergen have not advanced their departure from Scottish wintering grounds despite an advanced onset of spring at their Norwegian stopover site, in contrast to pink-footed geese, which largely share the same flyway and have advanced their spring migration (Tombre et al. 2008). Their study suggests that barnacle geese breeding at Spitsbergen cannot predict spring in Norway from their wintering site in the United Kingdom because of the large overseas crossing. The Russian breeding barnacle geese, however, do not have such a large overseas crossing, and prioritize other factors than responding to advanced onset of spring in the Baltic. Thus, although the timing of high quality food during migration is important for barnacle geese (Van der Graaf et al. 2006b), this result suggests that barnacle geese may prioritize other factors above the onset of plant growth in spring, and that the observed delay in migration cannot be caused by climatic changes. Theory also predicts that birds should not advance their timing of migration as much as spring advances, because the timing of migration has not only evolved to match the peak of food availability but also in response to many other factors, such as competition for territories and predation risk (Jonzén et al. 2007).

Our assumptions on decreased potential intake rates are supported by empirical studies

(Van der Graaf et al. ; Eichhorn). Both studies suggested a recent decrease in intake rates at a Baltic stopover site. Additionally, barnacle geese have been observed to colonize new staging sites at several locations in the Baltic. Populations staging at traditional sites remained approximately constant (Leito 1996), indicating that the traditional sites reached capacity, especially because the total population of geese increased much more than the population staging in the Baltic (Eichhorn et al. 2009). Besides, the ongoing urbanization in the Baltic region has led to a general decline in agricultural practice, e.g., cattle farming. Consequently, intake rates may also have decreased as facilitation by large grazers decreased. Altogether, decreased intake rates can be a plausible explanation for the observed delay.

In addition to the importance of food en route, our simulations showed a particularly strong effect of predation danger on the departure date from the wintering site. When predation danger in the Baltic was only slightly higher compared to the other sites, the geese immediately started delaying departure from the wintering site, reducing staging time at the dangerous site and ultimately, skipping the site with higher predation risk. This is in line with theoretical predictions that a migratory bird should minimize the time spent in a dangerous area (Houston 1998) and that the loss of future reproductive success by predation is traded off against the benefit of increasing reserves by foraging (McNamara and Houston 1994). Predators can have a strong influence on migratory strategies, e.g. by causing migrants to avoid the predator abundance peak (Lank et al. 2003). If the whole Baltic area has become more dangerous due to the recovery of predator populations, we expect the geese to minimize the time spent in that area. The strong increase in predator numbers such as white-tailed eagles *Haliaeetus albicilla* in the Baltic; a fourfold increase in Estonia (from 40 to 150-170 (Hermann et al. 2009)), Latvia and Finland and expansion into Gotland, Sweden (Helander et al. 2003), indicates that the Baltic has indeed become a more dangerous place for barnacle geese compared to the Netherlands. For example, on the island of Saaremaa (2,672km2), Estonia, which is a major stopover site in the Baltic, there are 28 known white-tailed eagle territories (pers. comm. V. Völke). Contrastingly, there is currently only a single breeding pair in the Netherlands (41,528km2). For this breeding pair it has been confirmed that it preys on greylag geese *Anser anser* (Roder et al. 2008).

Additionally, predation danger caused birds to not take full advantage of available resources, as they take the danger into account in their decision where to forage (Pomeroy et al.). These non-lethal effects of predation can potentially be larger than the lethal effects (Cresswell 2008). Hence, increased predation danger can reinforce the already existing effects of decreased intake rates. The influence of density-dependent effects on this trade-off is not immediately clear. Potentially, danger can cause many geese to shift to safer areas, thereby decreasing the competition for food in the dangerous areas. However, it is known that barnacle geese facilitate each other while grazing (Ydenberg and Prins 1981). Consequently, a dangerous and less grazed area does not necessarily lead to better feeding conditions. Our model did not take these density-dependent effects into account.

In conclusion, predation danger, in addition to food availability, can be a key factor in explaining the observed changes in migratory behaviour of barnacle geese. This study only approached the problem from a theoretical point of view, but identified critical factors to be studied empirically in the field. These new insights also suggest that challenging geese with natural predators in the Netherlands, e.g. by creating suitable nesting places for white-tailed eagles, may improve management of the agricultural conflict. Future empirical research needs to test our predictions by measuring the direct and indirect effects of predator activities on goose behaviour. Although this study focused on the case of the Barnacle Goose, its conclusions are not limited to goose migration. It is often assumed that timing of migration is synchronized with the phenology of resources (Visser and Both 2005), resulting in potential mismatches and associated population declines as a result of climate change (Jones and Cresswell 2010). These two studies state respectively that looking at predation in addition to resources as explanatory factor is very difficult or do not even mention predation at all as potential explanatory factor. We want to emphasize that in addition to currently well studied factors such as food availability and climatic change, predation danger should be considered in the suite of potential explanatory variables for changes in the migratory behaviour of birds.

Acknowledgements

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Observation tent at field work site near Rahuste, Estonia

Chapter 3

Divergence in timing of parental care and migration in Barnacle geese

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Abstract

In migratory geese, the extended association of parents and offspring is thought to play a crucial role in culturally transmitting the migration strategy to the next generation. Goslings migrate with their parents and associate closely with them almost until the next breeding season. Families do not break up until spring migration, when the parent-offspring conflict intensifies during preparation for the next generation of offspring. Recently, the commencement of spring migration of the Russian population of the Barnacle Goose has been delayed by about one month. Here we investigated whether the duration of parental care behaviour changed with this alteration in migratory behaviour. In contrast to our expectation, we found that parental care terminated well before the commencement of spring migration, and that parent-offspring associations were nearly absent during spring migration. We argue that the mechanisms for determining the duration of parental care is different from that determining the commencement of spring migration, hence, we conclude that a divergence in timing has developed between both behaviours. A consequence of this divergence could be that the cultural transmission of migratory behaviour is disrupted, possibly playing a role in the recent establishment of new populations of barnacle geese across the Russian flyway.

Introduction

Migration is an adaptation to maximize fitness in seasonally changing environments by selecting the best habitat throughout the year. Individuals need to base migratory decisions, such as when to start migration or where to stopover, on the temporal and spatial distribution of food and safety (Alerstam and Lindström 1990; Jonzén et al. 2007). Migration is most successful when an individual has information on when to be where. Timing and direction of migration are known to be influenced by the earth's magnetic field, photoperiod and/or polarized light (Alerstam et al. 2003) and the sensitivity for these cues is suggested to be genetically programmed. For example, studies on blackcaps *Sylvia atricapilla* showed that both the migratory restlessness (Berthold and Querner 1981) and the migratory direction (Helbig 1991) have a genetic basis.

In contrast, there are some species in which all migratory behaviour, including the decision on whether to migrate or not, is culturally determined. Consequently, individuals of these species can adapt better to environmental changes, than those that have genetically transmitted migration (Sutherland 1998). For example, herring *Clupea harengus* are suggested to develop migratory routines early in life by adopting the same migratory routine as their predecessors, even when the environment changes. Young herring adopt these routines due to their innate tendency to school with other, experienced herring (Corten 2002). A similar cultural transmission of migration is present in geese, and this has been shown in an experiment to “teach” lesser white-fronted geese *Anser erythropus* a new migration strategy to the Netherlands instead of to their original wintering grounds in Eastern Europe. To this end, barnacle geese *Branta leucopsis*, wintering in the Netherlands, were used as foster parents in Sweden and this resulted in lesser white-fronted geese adopting the migratory behaviour of these barnacle geese (Von Essen 1991). There are also cases known in which humans acted as foster parents and consequent migration “teachers” for canada geese *Branta canadensis* and trumpeter swans *Cygnus buccinator* (Sladen et al. 2002).

This cultural transmission of migration is possible because parental care and the accompanying parent-offspring association extents until during migration. It is widely accepted that one of the functions of this long parental care is to guide or teach the offspring the migration routes (Mayr 1942; Hochbaum 1955; Kear 1970; Owen 1977; Baker 1978; Owen 1980). For example, Kear suggests that: “*family life lasts longest in the migratory arctic-breeding swans and geese, who tolerate their young and indeed defend them, until the next breeding season. The group migrates together and this is probably extremely important in establishing traditional flight paths and feeding grounds*” (Kear 1970, p 374).

In barnacle geese that winter in the UK and migrate to breeding grounds on Spitsbergen, parental care lasts for approximately 9-10 months (Black and Owen 1989). The termination of the parent-offspring association coincides with the period of spring migration. Before migration, 20% of the young are not attached to any family, whereas the percentage of unattached young increases to 65% during migratory stopover (Black and Owen 1989). During the migratory stopover in Norway, parents sharply increase attacks towards offspring, suggesting that the extended parental care conflicts with the preparation for the next breeding attempt.

The population of barnacle geese breeding in Russia migrates in spring from wintering grounds in The Netherlands via a stopover in the Baltic to breeding grounds the Russian Arctic. The phenology of the Russian population was comparable to the Spitsbergen population until the 1990’s. That is, the timing of migration from the wintering area to the staging area, respectively Baltic or Norway, occurred in the first half of April (Owen 1980; Madsen et al. 1999), the migration from the staging area to the prebreeding area in Russia or Spitsbergen occurred in second half of May (Owen 1980; Leito 1996; Madsen et al. 1999), the arrival at the breeding area occurred in early June and breeding was initiated in both populations shortly after arrival at the breeding area (Syroechkovskiy et al. 1991; Madsen et al. 1999). We can also assume that the timing of parental care was similar for these populations (Owen 1980), which is supported from observations of families during spring migration in Estonia (Leito 1996). Hence, we assume that the timing of parental care behaviour of the Russian population was comparable to the Spitsbergen population, and thus lasted until spring migration in April in the 1970-1980's.

The Russian population, however, has delayed commencement of spring migration with approximately one month over the past two decades (Eichhorn et al. 2008; Jonker et al. 2010). We thus asked whether the timing of the termination of parental care changed in parallel to the change in timing of spring migration in Russian breeding barnacle geese.

Because barnacle geese have shown various changes, such as a reduction in clutch size (Eichhorn et al. 2010) and an advancement of laying date (Van der Jeugd et al. 2009), in response to changes in their migratory behaviour, we hypothesize that the termination of parental care has delayed with one month, and that parental care thus still lasts until during migration. We tested this hypothesis by recording the attachment of offspring to a family in addition to comparing agonistic, vigilance and foraging behaviour of parents and non-parents.

Methods

We observed barnacle geese during autumn migration of 2008, winter of 2008-2009, and spring migration of 2009 over 6 observational periods (Table 3.1). We selected a migratory stopover area on the island of Saaremaa in Estonia (58° 05' N, 22° 06' E), hosting approximately 10,000 barnacle geese in autumn and spring. The site for winter observations in the north of the Netherlands (53° 02' N, 5° 25' E) was designated as a goose accommodation area for approximately 40,000 barnacle geese.

Table 3.1. Overview of the date, place and number of observations per category.

Dates	Place	Parents	Non-parents
15-30 October 2008	Estonia	135	142
17-28 November 2008	The Netherlands	34	34
15-20 December 2008 & 11-19 February 2009	The Netherlands	39	52
11-19 March 2009	The Netherlands	21	49
6-16 April 2009	The Netherlands	26	55
6-21 May 2009	Estonia	10	348

The average length of our remaining protocols was 8.4 minutes, and the median length was 10 minutes over 945 protocols.

We observed geese with and without goslings, hereafter called 'parents' and 'non-parents' respectively, and quantified parental care as the behavioural difference between the two groups. Adults and goslings were identified using the description of Svensson et al. (1999). To determine parental status, we observed an adult goose for up to ten minutes until we were sure whether there were goslings attached or not. We then continuously observed the focal individual up to ten minutes recording behaviour with a Psion Workabout MS (RACO Industries, Cincinnati, Ohio, USA) and Noldus Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands). We categorized behaviour as 'foraging', 'vigilance', 'walking', 'preening', 'resting', 'attacking' and 'other'. Additionally, whether goslings were attached to a family or not was noted every day from February onwards. A test with four observers observing a filmed protocol independently, showed that the standard deviation around the estimated mean percentage for both foraging and vigilance was smaller than one percent.

Of the behavioural categories, foraging, vigilance and attacking are considered most important for parental care in barnacle geese (Black and Owen 1989) and we thus restricted analyses to these behaviours. Non-parents always greatly outnumbered parents, and to balance observations we first searched for parents. This became more difficult as the season progressed (as indicated by the sample sizes in Table 3.1). Ringed individuals were few, and we thus used mainly observations of un-ringed birds.

Statistical analysis

We calculated for each observation the proportion of time foraging, the proportion time being vigilant, the mean foraging bout length, mean vigilance bout length and the number of attacks. We excluded as unreliable all (22) observations shorter than two minutes.

Because we defined parental care as the difference in behaviour between parents and non-parents, and because not only the behaviour of the parents changed during the season but also that of the non-parents, we also used an measure of difference between parents and non-parents for each observation, hereafter called residual vigilance or residual foraging. For this residual foraging or vigilance, the behaviour of the non-parents was used as a base-line. For example, the residual vigilance (R_V, with sub-script V for vigilance and subscript F for foraging) is calculated as:

$$R_V = V_p^{parent} - \overline{V}_p^{non-parent} \qquad eqn.\ 3.1$$

, where p is observation period, V_p^{parent} is the vigilance of an observation of a parent in period p, and $\overline{V}_p^{non\text{-}parent}$ is the mean vigilance of all non-parents for that period. So each observation now had, in addition to a percentage foraging or vigilant, a measure for the difference between parents and non-parents, relative to the non-parents, where the

mean R_V per period for the non-parents was obviously zero. For each period, we tested for differences in vigilance and R_V, between parents and non-parents with an independent sample t-test for unequal variances (see Table 3.2) and a Bonferroni correction.

To compare the number of attacks we used a linear model with number of attacks per minute as response variable and parental status, period, and the interaction term as predictor variables. Additionally, we tested post hoc for each period whether there was a difference in number of attacks per minute between 'parents' and 'non-parents' with a Welch t-test for unequal variances.

We analysed the attachment of offspring to a family with a generalized linear model for binomial distribution and logit-link function, with attachment as binomial response variable and period as predictor variable. Additionally, we did a post-hoc analysis with a Bonferroni correction, using a binomial test. We used a log-normal regression to test the effect of time and parental status on foraging and vigilance bout lengths. Furthermore, we used an independent sample t-test for unequal variances to test whether the length of a foraging bout or vigilance bout were different for 'parents' and 'non-parents' in each 'period'. Statistical tests were performed with *R* (*R* Development Core Team, 2009).

Table 3.2. Test results for vigilance and R_V in each period between parents and non-parents.

		Vigilance			R_V	
Period	**t**	**d.f.**	**p**	**t**	**d.f.**	**p**
October	-9.382	218.90	< 0.001	-9.382	218.90	<0.001
November	-5.0217	65.75	< 0.001	-5.0217	65.75	<0.001
December -February	-3.6048	67.51	< 0.001	-3.6048	67.51	<0.001
March	-0.4653	43.27	0.6441	-0.4653	43.27	0.644
April	-1.095	40.14	0.28	-1.095	40.14	0.28
May	-0.7547	9.17	0.4694	-0.7595	9.17	0.467

Test results are from Welch *t*-test from package '*stats*' in *R*.

Results

Vigilance was significantly influenced by the interaction between time of year (period) and parental status (linear model: R^2-adj.: 0.16, $F_{3,940}$: 58.71, $p<0.0001$; interaction 'period-parental status': estimate: -3.38, std. error of estimate 0.72, t: -4.67, $p< 0.0001$). Parents were vigilant for 34% of the time in October, whereas non-parents were only vigilant for 13 % of the time. In November parents were still more vigilant than non-

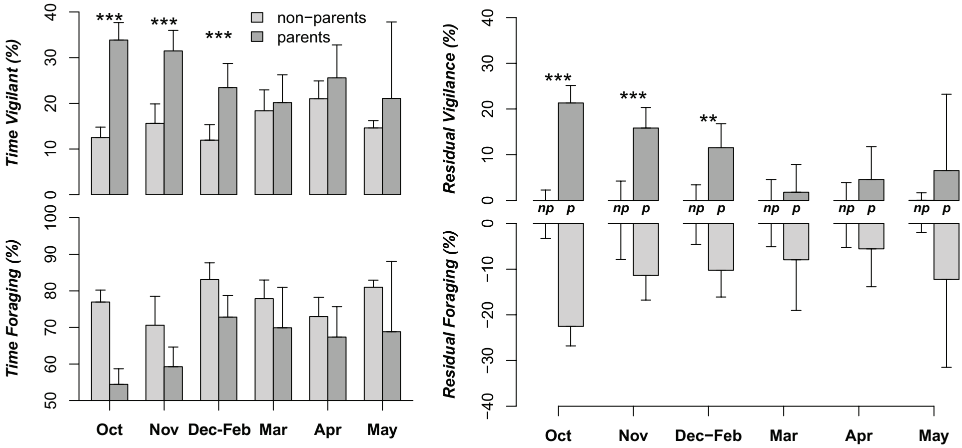

Figure 3.1. Foraging and vigilance parents and non-parents.
The percentage of time spent on foraging and vigilance per period for parents and non-parents (left). Mean residual vigilance and foraging per period for parents (p) and non-parents (np) (right). The error bars show 95% confidence intervals. Significance levels indicate the p-values from the t-test between parents and non-parents within each period: ***= p<0.001, **= p<0.01, *=p<0.05.

parents, with 31% vs. 16%. During winter (December-February) parents were less vigilant than before, but still more vigilant than non-parents (23% vs. 12%). From March onwards there was no difference in vigilance between parents and non-parents (March: 20% vs. 18%, April: 26% vs. 21%, May: 21% vs. 15%) (see Figure 3.1a and Table 3.2 for summary). Because foraging and vigilance were dependent on each other an increase in vigilance resulted in an approximately similar decrease in foraging time for parents.

The residual vigilance (R_V) was significantly influenced by the interaction between time of year (period) and parental status (linear model: R^2-adj.: 0.18, $F_{3,940}$: 70.66, $p<0.0001$; interaction 'period-parental status': estimate: -4.29, std. error of estimate 0.72, t: -5.97, $p< 0.0001$). The R_V was 21 during autumn migration in October, indicating that the difference in time vigilant between parents and non-parents was 21% of the total time budget. In November R_V had decreased to 15 and during winter (December-February) R_V decreased to 11 which was still significantly different from zero.. From March onwards R_V was no longer statistically different from zero (see Figure 3.1b and Table 3.2 for summary). An indication for the presence of parental care is the effort it took to find actual parents. One can see (Table 3.1) that the number of observations of parents started to decrease from February onwards. From March onwards it took great effort to find the few parents we observed, and during spring migration in May there were hardly any parents, leading to the unbalance between parents and non-parents in our data in those periods. The search effort to balance the data resulted in a bias towards parents, which is for our question a conservative bias, indicating that parental care certainly did not last longer than we now observed.

The mean number of attacks per minute was significantly influenced (at the 0.10 level) by the interaction between the parent status and period of observation (linear model: R^2-adj: 0.014, $F_{3,940}$: 5.49, $p<0.001$; interaction: estimate: -0.012, st.error of estimate: 0.006, $p = 0.07$). The low R^2 is caused by the large number of zero's in the data. In October, parents had an attack rate of 0.07 times per minute, against 0.02 for non-parents. In November, parents attacked 0.05 times per minute, against 0.01 for non-parents. During winter, from December until February, parents attacked with 0.13 attacks per minute significantly more than non-parents with 0.01 attacks per record. From March onwards, the number of attacks per minute did not differ between parents and non-parents (Figure 3.2, see Table 3.3 for statistical details).

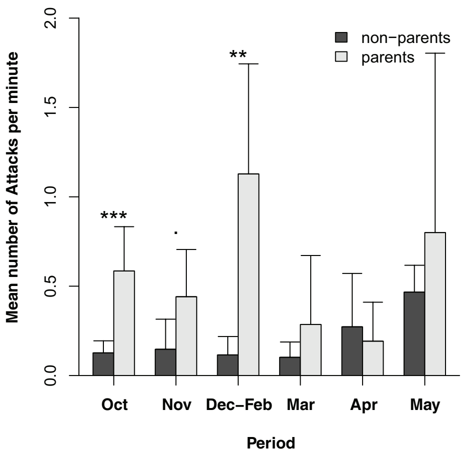

Figure 3.2. Attacks.
The mean number of attacks per observation for parents and non-parents per period. Error bars show 95% confidence intervals. Significance levels indicate p-values from the t-test between parents and non-parents within each period: ***= $p<0.001$, **= $p<0.01$, *=$p<0.05$.

Table 3.3. Test results for number of attacks per minute between parents and non-parents within each period.

	Attacks per minute		
Period	**t**	**d.f**	**p**
October	-3.3684	185.135	<0.001
November	-1.9032	55.39	0.062
December -February	-3.1402	41.078	0.003
March	-0.9106	21.995	0.372
April	0.3063	77.15	0.760
May	-0.4654	9.698	0.652

Test results are from Welch t- test from package 'stats' in *R*.

Log-linear model analysis showed that the length of foraging bouts and the length of vigilance bouts was significantly influenced by the interaction between period and parental status (foraging: R^2-adj.: 0.15, $F_{3,934}$: 56.77, $p<0.0001$; interaction 'period-parental status': estimate: 0.11, std. error of estimate 0.03, t: 4.0, $p< 0.0001$; vigilance: R^2-adj.:

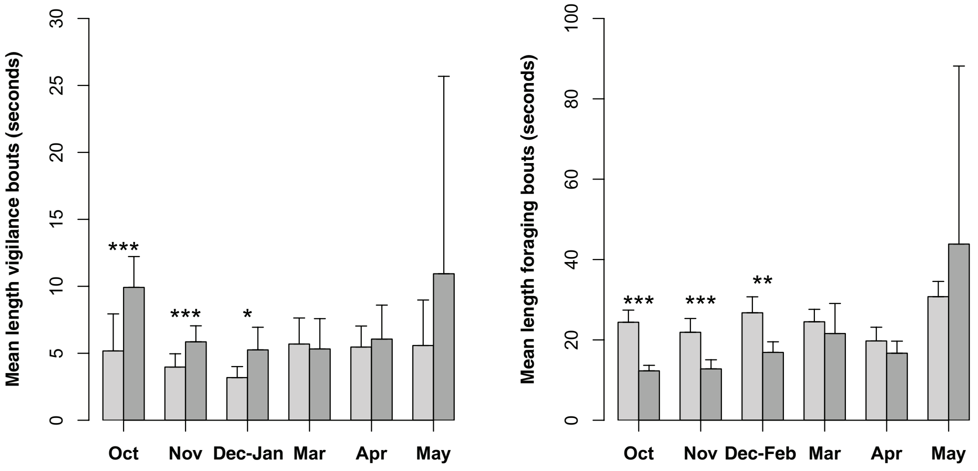

Figure 3.3. Vigilance and foraging bouts.
The mean bout length for vigilance (left) and foraging (right) for parents (dark grey) and non-parents (light grey) per period. Error bars show 95% confidence intervals. Significance levels indicate p-values from the t-test between parents and non-parents within each period: ***= p<0.001, **= p<0.01, *=p<0.05.

0.08, $F_{3,940}$: 30.83, p<0.0001; interaction 'period-parental status': estimate: -0.09, std. error of estimate 0.04, t: -2.6, p< 0.01). The mean vigilance bout length was significantly longer for parents with 9.9 seconds than for non-parents with only 5.2 seconds in October. Also foraging bout lengths were different, with 12.3 and 24.4 seconds for parents and non-parents respectively. During November, both vigilance (5.9 vs. 4) and foraging (12.8 vs. 21.9) bout lengths were different, as well as from December until February (vigilance: 5.3 vs. 3.2, foraging: 16.9 vs. 26.8). From March onwards the length of both vigilance (March: 5.3 vs. 5.7 ,April: 6.1 vs. 5.5, May: 10.9 vs. 5.6) and foraging (March: 21.6 vs. 24.5 ,April: 16.7 vs. 19.7, May: 43.9 vs. 30.8) bouts was statistically the same for parents and non-parents (Figure 3.3, see Table 3.4 for statistical details). Note that in contrast to mean percentage of time spent on foraging or vigilance, the length of both foraging and vigilance bouts can increase, because they are not dependent on each other. The percentages of unattached and attached offspring were equal in February, although this equality was influenced by our search bias towards attached offspring. Afterwards, the percentage of unattached offspring rapidly increases (Figure 3.4).

Discussion

Our results on vigilance, foraging, residual vigilance, attacks and bouts all show that parental care lasted until February. Our use of a measure for the difference between parents and non-parents helps to see what parents do, in case of vigilance, or do not, in

case of foraging, compared to non-parents. Aided by the absolute time spent on vigilance and foraging, it gives good insight in the efforts parents make for their offspring. The added value of using a R_V is that it allows for, for example, comparison of different populations because the behaviour of non-parents is used as a base-line. These results are supported by our observation that the number of offspring unattached to a family greatly increased after February. In contrast to earlier studies that showed that parental care in barnacle geese lasted until during migration (Black and Owen 1989), we show that parental care, and thus parent-offspring association, in Russian breeding barnacle geese currently does not last until during migration. Actually, where the commencement of spring migration has delayed from April to May, termination of parental care has advanced from April to (the end of) February, resulting in a two month gap between the end of parental care and the beginning of spring migration. That both timing of termination of parental care and commencement of spring migration are diverging from a formerly overlapping situation, and thus no longer overlap or match phenologically, suggests that the timing of these behaviours is regulated by different mechanisms. From other Anatidae, such as ducks, it is known that extended parental care is regulated by hormones such as prolactin (Boos et al. 2007), and other aspects of breeding in geese

Table 3.4. Test results for foraging and vigilance bout lengths between parents and non-parents within each period.

		Vigilance bouts	
Period	**t**	**d.f.**	**p**
October	-2.58	267.3	<0.05
November	-2.38	63.8	<0.05
December -February	-2.16	55.8	<0.05
March	0.24	49.2	0.81
April	-0.39	44.8	0.70
May	-0.69	10.0	0.50
		Foraging bouts	
Period	**t**	**d.f.**	**p**
October	7.14	193.9	<0.0001
November	4.34	55.7	<0.0001
December -February	4.05	84.1	<0.001
March	0.71	27.1	0.48
April	1.32	74.1	0.19
May	-0.58	9.1	0.58

Test results are from Welch t-test from package ‘stats’ in *R*.

are also regulated by prolactin (Jonsson et al. 2006). It thus likely that an innate mechanism, not connected to the mechanism determining commencement of migration, is regulating extended parental care. But because offspring is expected to disagree with the parents over termination of parental care (Trivers 1974), the behaviour of the offspring is suggested to also influence this termination (Black and Owen 1989). Experimental studies could provide insights in how the moment of family break-up can change.

There are some other examples of studies suggesting that changes in migration phenology have population consequences. Pied flycatchers *Ficedula hypoleuca*, for example, are constrained in their laying date by their arrival date in the Netherlands. This arrival date is constrained by their departure from wintering grounds in Africa, which are triggered by local climate variables. The changing conditions in The Netherlands require an advancement of laying date, but because the locale climate in Africa is not changing at the same rate as in The Netherlands, the arrival date cannot advance sufficiently (Both et al. 2006). Another example is that cuckoos *Cuculus canorus* are advancing their first arrival date, in response to climate changes, less than some of their host species. Because the arrival dates are a good predictor for laying dates and because cuckoos synchronize breeding with their hosts, cuckoos may miss breeding opportunities (Saino et al. 2009). Both studies suggest that this results in decreased reproductive success and ultimately a population decline. However, in our study system this is clearly not the case.

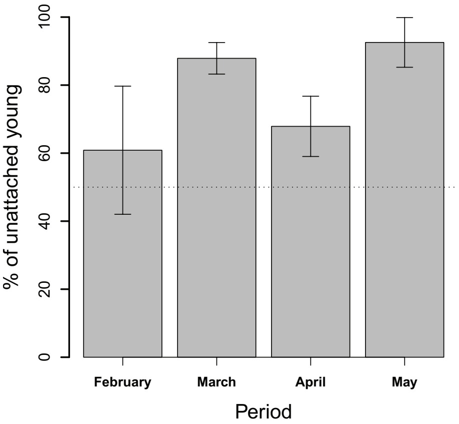

Figure 3.4. The percentage of unattached young.
The dotted line indicates the 50% line, which was our aim throughout the observations. Error bars show 95% confidence intervals.

Despite this divergence, Russian barnacle geese are very successful, which suggests that the assumed mechanism of teaching migration behaviour to offspring was either never present or not so important for successful migration as previously thought or has became less important, for this species. The data to support the long parental care or family duration of geese are very scarce (Prevett and MacInnes 1980; Black and Owen 1989) and yet it is often (Mayr 1942; Hochbaum 1955; Kear 1970; Owen 1977; Baker 1978; Owen 1980; Newton 2008) presented as an established fact. Our study suggests that this might not be as general as previously assumed, and studies on other species within the Anserinae, and on populations within these species with respect to parental care could clarify this issue.

Because the commencement of migration has delayed and the arrival on the breeding grounds has not (Eichhorn et al. 2006), the duration of migration has become shorter and more energetically costly (Hedenström 1992). Possibly, this has made time more valuable during migration and has changed the balance between the cost and benefits of extending parental care. Hence, making it no longer beneficial to extend parental care into migration. A possible consequence of this divergence can be that the migratory traditions are broken, as suggested by Owen: "*Most wildfowl are highly traditional, … , but how are these traditions maintained? Geese and swans are highly gregarious family birds and the adults and parents lead their inexperienced young during the first year of their life. The old geese may remember particular feeding fields or parts of fields. Once this tradition has been broken (…) young will not find their way automatically to suitable breeding grounds*" (Owen 1977, p 39). Although there are many other individuals in goose flocks to learn or copy migratory behaviour from, the chance that offspring will develop other migratory behaviour than their parents increases with an increasing time gap as a result of the divergence in timing of parental care and migration. We currently see many new migratory strategies emerging for barnacle geese, and the emergence of these strategies coincides with the delay in commencement of migration. In the 1980's a population was established on a former stopover site (Larsson et al. 1988), thereby shortening migration distance with almost 2000 km. Ten years later, a population was established in the former wintering site, the Netherlands (Ouweneel 2001), thereby stopping migration at all. Clear mechanistic explanations for these emergences have not been given yet, and the population genetics structure could help answering this question, as well as on how the three different flyways (Greenland, Spitsbergen, Russia) of barnacle geese have emerged historically. We argue that the potential disruption of transmission of migration strategy, as a result from a divergence between the commencement of spring migration and the end of parental care, can explain the emergence of new migration strategies in barnacle geese.

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Barnacle goose family in park Clingendael, The Hague, The Netherlands

Chapter 4

Rapid adaptive adjustment of parental care coincident with altered migratory behaviour

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Abstract

The optimal duration of parental care is shaped by the trade-off between investment in current and expected future reproductive success. A change in migratory behaviour is expected to affect the optimal duration of parental care, because migration and non-migration differ in expectations of future reproductive success as a result of differential adult and/or offspring mortality.

Here we studied how a recent emergence of non-migratory behaviour has affected the duration of parental care in the previously (until the 1980s) strictly migratory Russian breeding population of the Barnacle Goose *Branta leucopsis*. As a measure of parental care, we compared the vigilance behaviour of parents and non-parents in both migratory and non-migratory barnacle geese throughout the season. We estimated the duration of parental care at 233 days for migratory and 183 days for non-migratory barnacle geese. This constitutes a shortening of the duration of parental care of 21% in 25 years. Barnacle geese are thus able to rapidly adapt their parental care behaviour to ecological conditions associated with altered migratory behaviour. Our study demonstrates that a termination of migratory behaviour resulted in a drastic reduction in parental care and highlights the importance of studying the ecological and behavioural consequences of changes in migratory behaviour and the consequences of these changes for life-history evolution.

Introduction

Parental investment is widely studied because of its consequences for reproductive success. From Trivers' definition of parental investment: 'any investment by the parent in an individual offspring that increases the offspring's chance of surviving (and hence reproductive success) at the cost of the parent's ability to invest in other offspring' (Trivers 1972, p. 67), the trade-off between investment in current reproductive success and in expected future reproductive success is evident (Figure 4.1). The trade-off is shaped by the opposing effects of further investment on current and expected future reproductive success. The level of investment maximizing lifetime reproductive success occurs at the point that the marginal benefit of further investment in terms of current reproductive success is offset by marginal cost in terms of expected future reproductive success. Differences in life-style or environment that affect the marginal costs or benefits of investment are expected to cause differences in parental care behaviour (Clutton-Brock 1991).

Migration is behaviour typically associated with high rewards and high risks to future breeding opportunities as compared to non-migration and as such alters the balance between investment costs and benefits. Migration comes with costs, in terms of increased energy expenditure but also in terms of survival: during migration animals face a higher risk of predation, they have a higher risk of starvation because the resource availability during migration is hard to predict and they can lose their way. Several studies show that the period of migration has a much higher mortality than the period of non-migration. For example, black-throated blue warblers *Dendroica caerulescens* experience a 15 times higher mortality rate during the migratory season than during the non-migratory season, and more than 85% of the annual mortality occurs during migration (Sillett and Holmes 2002). These costs are presumed to be offset by benefits to current reproduction such as decreased nest predation risk (e.g. McKinnon et al. 2010) or higher offspring quality. Here we show how the altered costs and benefits affect parental investment decisions in the Barnacle Goose *Branta leucopsis*.

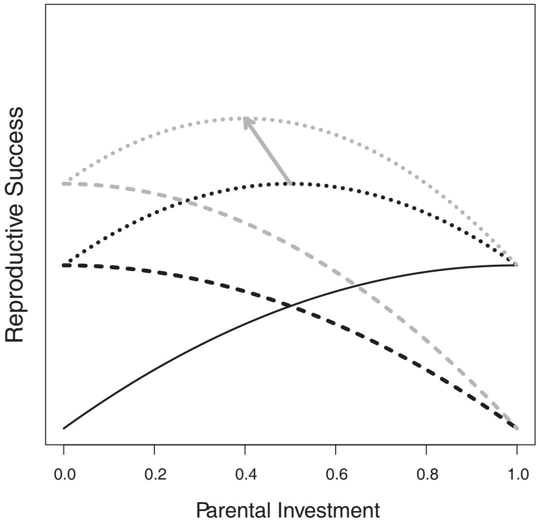

Figure 4.1. Trade-off between current and future reproductive success
Graphical representation of the trade-off between current and expected future reproductive success. The solid line is the current reproductive success with increasing investment in current offspring *C(i)*. The dashed line is the expected future reproductive success with increasing investment in current offspring *F(i)*. The dotted line is the sum of both C(i) and *F(i)*, equalling expected lifetime reproductive success *T(i)*. The marginal benefit (increase in current reproductive success) declines with investment, while the marginal cost (decrease in future reproductive success) increases with investment. The grey line portrays an environmental change, so that the expected future reproductive success resulting from any level of investment is higher. With more future at stake (i.e. *F(i)* is everywhere higher), the rate of increasing marginal costs of investment in current offspring has increased (i.e., steeper cost curve) causing a shift to lower levels of investment. The 2nd differential of *F(i)* equals R_{mc}, whereas the 2nd differential of *C(i)* equals R_{mb}.

The population of barnacle geese wintering in The Netherlands provides us with the unique situation of distinct migratory and non-migratory (sub-) populations within the same geographical area, allowing a comparison of migration and non-migration. The migratory sub-population breeds in Russia, migrating to and from The Netherlands via staging sites in the Baltic Sea (Ganter et al. 1999). The non-migratory sub-population resides in the Netherlands year round, has only emerged in the 1980s (Ouweneel 2001) and is growing rapidly (Van der Jeugd et al. 2009). Because the non-migratory population only recently emerged, presumably from the migratory population (see chapter six), this allows testing how parental care in natural populations is affected by changing ecological circumstances, which is important for understanding the evolution of parental care (Clutton-Brock 1991).

Geese have extended parental care behaviour which lasts until long after fledging. Geese provide parental care by increasing vigilance to protect offspring against predation and competition of conspecifics. They are among the very few avian species in which parents and offspring stay together for nearly a year (Mayr 1942; Kear 1970), with the termination of parental care taking place during spring migration preceding the breeding season (Black and Owen 1989). Additionally, the extended period of parental care supposedly plays an important role in the social structure of the populations (Van der Jeugd et al. 2002) and in the cultural transmission of migratory behaviour (Owen 1980). As in other (groups of) species such as meerkats *Suricata suricatta* and corvids, extended duration of parental care functions as a period to socially transmit important skills, such as foraging or vigilance (Clayton and Emery 2005; Thornton and McAuliffe 2006; Graw and Manser 2007). This underlines the potential importance of an effect of migratory change on parental care behaviour in geese.

Here we study whether this recent change in migratory behaviour influences the parental care behaviour of barnacle geese. Based on the effects of non-migratory behaviour on both the costs and benefits of parental investment, we predict shorter parental care in the non-migratory than the in migratory sub-population. First, the lower mortality (and hence greater expected future) of non-migrants, results in a higher rate of increasing marginal costs of investment (R_{mc} ; see Figure 4.1 for schematic overview and Figure 4.2 for predictions). Second, the higher offspring survival of non-migrants results in a lower rate of decreasing marginal benefits (R_{mb} ; Figure 4.2). Juvenile survival, based on ring resightings, is 0.55 for the offspring of migratory and 0.97 for offspring of non-migratory individuals (Van der Jeugd et al. 2009). Thus, increased investment by non-migratory geese can hardly increase offspring survival, making the marginal benefit of investment smaller (i.e., lower rate of decreasing marginal benefits and a more shallow benefits curve) for non-migratory than for migratory barnacle geese. The interaction of various cost and benefit scenarios and the consequent optimal level of parental investment are visualized in Figure 4.2.

Both the higher marginal costs and lower marginal benefits of non-migration separately predict lower parental investment in non-migratory barnacle geese, and when combined the difference is predicted to be even larger, as we assumed these effects are additive. To test this prediction, we studied how long barnacle geese provide parental care in the migratory and non-migratory population.

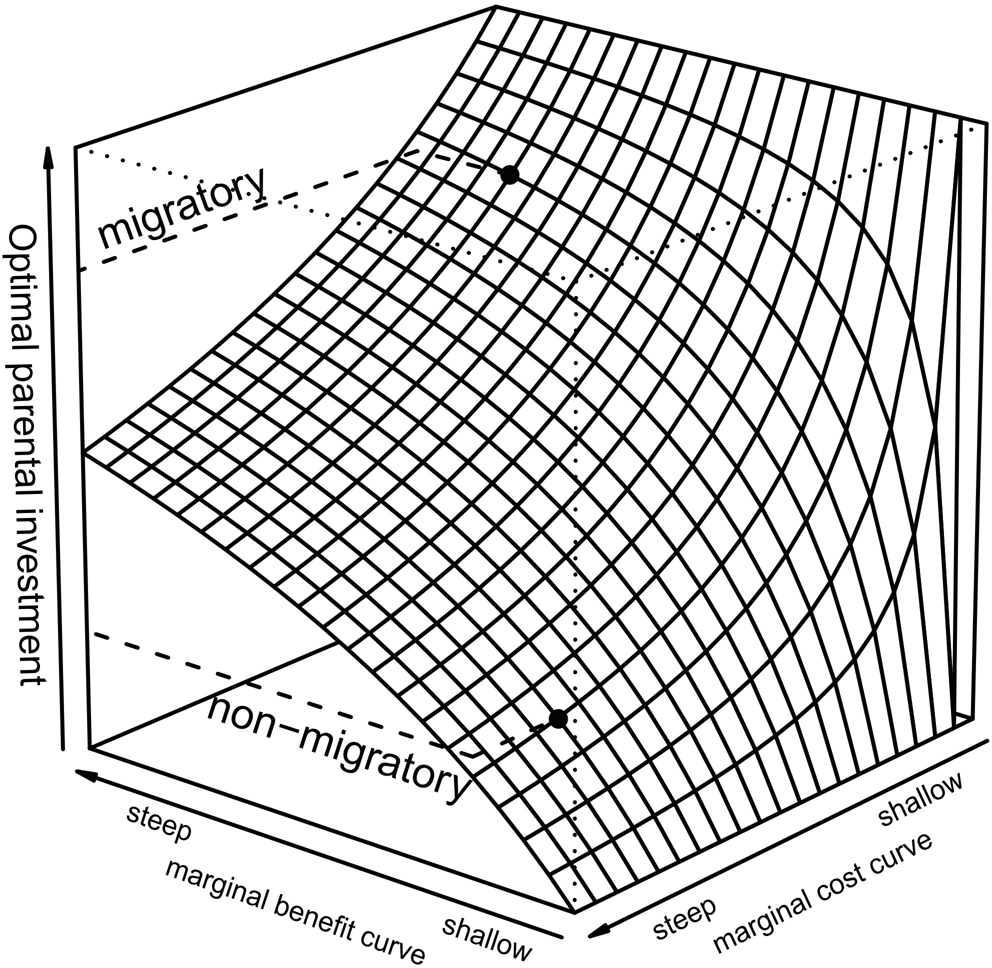

Figure 4.2. Predicted level of parental investment
Prediction of optimal level of parental investment with changing rate of increasing marginal costs (R_{mc}), and changing rate of decreasing marginal benefits (R_{mb}). The surface indicates the level of investment giving maximum expected lifetime reproductive success (I^*) and is calculated by taking the maximum of *T(i)* of Figure 4.1 (being the sum of *C(i)* & *F(i)*) (as the maximum life time reproductive success is the point where the marginal benefits and marginal costs are equal), resulting in equation 4.1. Dots indicate hypothetical positions of migratory and non-migratory populations and our prediction for parental investment in these populations.

$$I^* = \frac{R_{mb}}{R_{mc} + R_{mb}} \qquad eqn.\ 4.1$$

Methods

To quantify parental care behaviour we observed migratory and non-migratory barnacle geese. We observed migratory geese during migratory stopover (October 2008 and May 2009) on the island of Saaremaa in Estonia (58° 05' N, 22° 06' E), hosting approximately 10,000 barnacle geese in autumn and spring. We observed the migratory population

Table 4.1. Overview of observations.

Population	*Period*	*dates*	*Total samples*	*parents/non-parents*
Migratory	October	17/10 – 29/10	277	135 / 142
	November	18/11 – 28/11	68	34 / 34
	December – February	17/12 – 19/2	91	39 / 52
	March	11/3 – 19/3	70	21 / 49
	April	6/4 – 16/4	81	26 / 55
	May	7/5 – 19/5	358	10 / 348
Non-migratory	October	5/11 – 14/11	42	18 / 24
	November	2/12 – 11/12	54	29 / 25
	December – February	6/1 – 6/2	44	19 / 25
	March	25/2 – 5/3	78	38 / 40
	April	26/3 – 2/4	86	43 / 43
	May	21/4 – 29/4	77	22 / 55

during winter and spring (November 2008 – April 2009) in the northern part of The Netherlands (53° 02’ N, 5° 25’ E). We observed non-migratory geese in the southern part of the Netherlands near the Krammersche Slikken (51° 40’ N, 4° 13’ E) from November 2008 until April 2009. The distance between the observation locations in the Netherlands is approximately 170km. We alternated observation periods between the migratory and non-migratory sub-populations, which resulted in six periods (Table 4.1), named after the months for convenience. We used observations of ringed individuals to validate the migratory or non-migratory status of observed individuals. In the non-migratory observation area, 95.5% (85/89) of the observed ringed individuals had been ringed during the breeding season in the Netherlands. In the migratory observation area in the Netherlands, 97% (35/36) of the ringed individuals had been ringed either on the Russian (Van der Jeugd et al. 2003) or at the Baltic breeding area (Larsson et al. 1988).

We observed geese with and without goslings, hereafter called ‘parents’ and ‘non-parents’ respectively, and quantified parental care based on the behavioural differences between the two groups. Adults and goslings were identified following Svensson et al. (1999). To determine parental status, we observed an adult goose for up to 10 min, to determine whether there were goslings attached or not. We then observed the focal individual again up to 10 min, recording behaviour with a Psion Workabout MS (RACO Industries, Cincinnati, Ohio, USA) and Noldus Observer 5.0 (Noldus Information Technology, Wageningen, The Netherlands). We categorized behaviour as ‘foraging’, ‘vigilance’, ‘walking’, ‘preening’, ‘resting’, ‘attacking’ or ‘other’ behaviour. We quantify parental care by comparing the vigilance behaviour. Vigilance is an often used measure for parental care in geese (Black and Owen 1989) and swans (Scott 1980). In a previous study on this system, we showed that the percentage of unattached goslings quickly increased after the difference in vigilance between parents and non-parents disappeared (Jonker et al. 2011, chapter 3).

Statistical analysis

We calculated for each focal sample the proportion of time spent vigilant. Vigilance and foraging together add up to approximately 90% of the time budget of geese (Black and Owen 1989), and are strongly and inversely related. We therefore use the percentage of time vigilant as our measure of the time budget. The behaviour of both parents and non-parents changed during the season, and so we defined parental care as the extra vigilance carried out by a parent relative to that of non-parents of the same sub-population (Jonker et al. 2011), hereafter called residual vigilance R_V, calculated as:

$$R_V = V_p^{parent} - \overline{V}_p^{non-parent} \qquad eqn.\ 4.2$$

, where p is observation period, V_p^{parent} is the percentage of time vigilance of an observation of a parent in period p, and $\overline{V}_p^{non-parent}$ is the mean vigilance of all non-parents for that period. By using the difference between parents and non-parents we could control for potential site-specific differences in vigilance behaviour. The R_V allows statistical comparison between the two populations. For graphical representation we use the raw data of vigilance and foraging. We used a linear model to test for the effect of parental status, migratory status, group size, period of the year (and all possible interactions between these variables) on the R_V and selected models by stepwise AIC comparison (function step in *R*). Subsequently we tested for differences in R_V between parents and non-parents in every period for both the migratory and non-migratory sub-populations, using an independent samples t-test for unequal variances, and used a Bonferroni correction for multiple comparisons. To estimate the termination of parental care, we used the date half way between the end of the last observation period with significant parental care and the beginning of the first period without parental care.

Results

As stated previously, vigilance and foraging are strongly and negatively correlated, and together constitute about 90% of the time budget. Consequently, any decrease in time spent vigilance corresponded with an equal increase in foraging time (Figure 4.3). There was significant parental care in the migratory sub-population until February, but in the non-migratory sub-population only until November, indicated by a significant interaction between period of the year, parental status and migratory status on the difference in vigilance between parents and non-parents (R_V) in the linear model (see Table 4.2 for

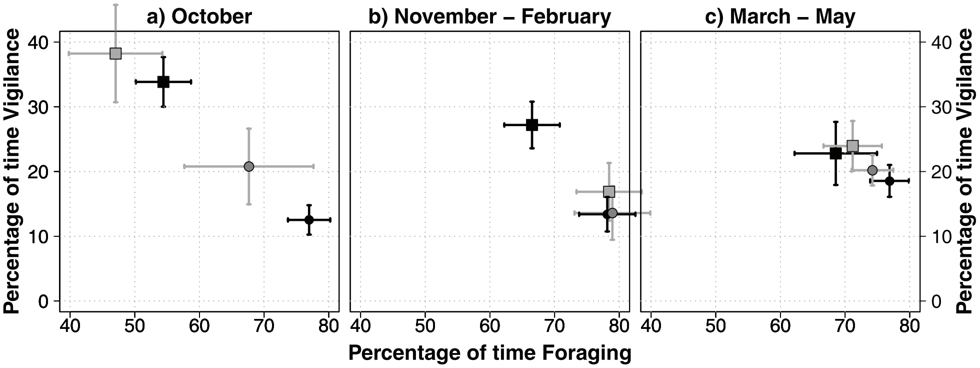

Figure 4.3. Temporal development of foraging and vigilance behaviour. The percentage of time being vigilant against the percentage of time foraging of parents (squares) and non-parents (circles) for three periods. In the first graph (a, October, period 1) there is significant parental care in both the migratory (black) and non-migratory (grey) population, in the second graph (b, November – February, period 2+3) there is parental care only in the migratory population, in the third graph (c, March – May, period 4-6) there is no parental care in either sub-population. Because of unevenness of number of observations of non-parents between period 4 and 5 and period 6, we used a random sample of the data from period 6, approximately equal to the sample sizes in period 4 and 5, for the graphical representation. Figure 4.3a: N parents migratory (N_{pm}): 135, N non-parents migratory (N_{npm}): 142, N parents non-migratory (N_{pnm}): 18, N non-parents non-migratory (N_{npnm}): 24. Figure 4.3b: N_{pm}: 73, N_{npm}: 86, N_{pnm}: 48, N_{npnm}: 50. Figure 4.3c: N_{pm}: 57, N_{npm}: 157, N_{pnm}: 103, N_{npnm}: 138. Error bars show 95% confidence intervals.

model results). This is illustrated in Figure 4.3 as follows: in the migratory sub-population, the percentage of time vigilant is twice as high for parents (33.84%) as for non-parents (12.52%) in October. In this period, in the non-migratory population, parents (38.22%) were also more vigilant than non-parents (20.78%) (Figure 4.3a, Table 4.3). From November until February parents (27.18%) were more vigilant than non-parents (16.86%) only in the migratory population, whereas vigilance levels were equal in the non-migratory population (13.59% vs. 13.40%) (Figure 4.3b, Table 4.3). From March onwards there was no difference in vigilance between parents and non-parents in either sub-population (migratory: 22.79% vs. 18.55%; non-migratory: 23.94% vs. 20.20%) (Figure 4.3c, Table 4.3). No interactions including group size significantly influenced the R_V. The use of a linear model was justified because the residuals approximated a normal distribution.

The termination of parental care was estimated for the migratory sub-population at February 28, against November 23 for the non-migratory sub-population. After correction for the difference in mean hatch date, which is July 11 for the migratory and May 25 for the non-migratory sub-population (Van der Jeugd et al. 2009), parental care lasts approximately 183 days for non-migratory against 233 days for migratory barnacle geese.

Discussion

The non-migratory sub-population of the Barnacle Goose emerged only approximately 25 years ago presumably from the migratory population (Meininger and Van Swelm 1994). Our results show that parental care in these non-migrants is much shorter than in the migratory sub-population (183 vs. 233 days). Even though we still found parents after the termination of parental care, the effort needed to find these individuals greatly increased after this termination (see chapter three). The difference constitutes 21% of the current duration of parental care of the migratory sub-population. An earlier study on the parental care duration of this migratory population of barnacle geese suggests that the duration of parental care has shortened as compared to 30 years ago (chapter three). In our study we assume that the Dutch non-migratory population originates from the Russian migratory population and recent genetic analysis confirms this assumption (chapter six). Assuming that, before the emergence of the non-migratory sub-population, parental care in the migratory sub-population lasted at least until the commencement of spring migration (Kear 1970; Black and Owen 1989), which was approximately mid-April in the 1970s (chapter two), the difference between the current duration of parental care in the non-migratory sub-population (183 days) and the assumed duration of parental care in the 1970s (279 days) is even larger, viz. 96 days, which amounts to a reduction of 34% of the 'original' duration.

Table 4.2. Results stepwise linear model RES_V

The model that was selected from a stepwise selection method based on AIC using the step function in *R*. The full model includes the factors: period (period of the year), population (migratory or non-migratory), parental status (parent or non-parent) and group size, including all interactions between these factors.

Dependent variable: RES_V	*Estimate*	*Std. Error*	*t value*	*Pr(>|t|)*	
(Intercept)	3.15E-01	1.09	0.289	0.77287	
period	7.58E-02	2.26E-01	0.335	0.73769	
population	6.41E-01	2.34	0.274	0.78417	
parental status	1.82E+01	1.74	10.498	< 2E-16	***
group size	-7.46E-04	3.10E-04	-2.403	0.01639	*
population* parental status	-1.03E+01	3.54	-2.904	0.00375	**
period* population	-2.39E-01	5.30E-01	-0.45	0.65297	
period* parental status	-3.11	5.26E-01	-5.913	4.32E-09	***
period*population*parental status	2.14	9.06E-01	2.362	0.01834	*

Residual standard error: 11.58 on 1272 degrees of freedom

Multiple R-squared: 0.1482, Adjusted R-squared: 0.1429

F-statistic: 27.67 on 8 and 1272 d.f., p-value: < 2.2E-16

To put this rate of change in perspective we calculated the rate of phenotypical change in darwins (Haldane 1949). This method allows to compare rates of relative phenotypic change over a given time period, corrected for the measurement interval. For example, when one bone length has increased by 10% and another by 20% in a million year (the example given by Haldane), one can use the darwin to compare these rates. Here the phenotypic change is from 233 to 183 over 25 years, resulting in 9662d. When this rate of phenotypic changes is corrected for the time scale of the change (Gingerich 1983), it results in 9.17d (with ln(time of change) being -10.6), which fits the pattern of rates of phenotypical change in colonization events (Category II in Figure 1 and Table 1 in Gingerich 1983).

A well-known example of behavioural adaptation to a new environment that differs in mortality is that of guppies introduced to an environment with different predators adapted their parental investment to producing fewer and larger offspring (Reznick and Endler 1982; Reznick et al. 1990). Using the results on the change of reproductive allotment of the introduction experiment of Reznick and Endler gives a rate of change of 118900d (time scale corrected: 11.7d with ln(time of change) being -12.9). Another more recent example of phenotypic change in response to a changed environment is that several species of songbirds have responded to afforestation by adapting their wing morphology (Desrochers 2010). The rate of change expressed in darwins for this study equals 968d (time scale corrected: 6.9d with ln(time of change) being -9.2). So, we cannot exclude that the rate of change in duration of parental care demonstrated in our study is caused by evolution.

When we look at the patterns of parental care in the Anatidae, a striking feature is that geese and swans provide long parental care. Most of the other Anatidae groups provide short parental care and the long (bi)parental care is considered to be the ancestral form of parental care in this family (Kear 1970). The pattern of adaptive radiation of parental care seems to match with the phylogeny of the Anatidae (Gonzalez et al. 2009). Apparently the pattern of long parental care was always very stable in this group. We now observe this rapid change in parental care duration in barnacle geese coincident with altered migratory behaviour. This raises questions whether similar changes are possible too in other species within the family and whether this assumed apparent stability of parental care duration is valid at all.

In ducks it has been shown that post hatching parental care is regulated by high levels of prolactin (Boos et al. 2007), which in turn seems to have a genetic basis in geese (Jiang et al. 2009). Future common garden experiments could elucidate whether this change in parental care is caused by phenotypic plasticity or evolution. Based on our study, we cannot discriminate between these two mechanisms.

To understand the implications of this change, we need to address the functional aspects of extended parental care in geese. In other animals, such as corvids, long periods of parental care allow offspring to copy foraging skills from parents, and hence increase parents' fitness via increased survival chances of the offspring (Clayton and Emery 2005). It is known from geese that in the first weeks after hatching parents assist their offspring with finding the best plants to eat by allowing them to forage form the same tussock of grass or even the same plant ('food sharing' according to Black and Owen 1989). However, whether this is a kind of provisioning or teaching is unclear, but this behaviour does not last long enough to explain the duration of parental care in geese. An obvious benefit for caring for offspring as long as geese do is that it provides protection for offspring against potential predators and competition by the increased vigilance level of the parents. In Bewick Swans *Cygnus bewickii*, parental care during winter protects offspring from competition with conspecifics, which can have far stretching consequences as the conditions experienced in the first year are crucial for future breeding and survival changes of the offspring, especially as the time available for foraging becomes limiting as a result of the short days in winter (Scott 1980). Additionally, the parents also benefit directly from the presence of offspring during migration because they are suggested to assist their parents in claiming the most profitable foraging patches (Loonen et al. 1999).

Table 4.3. Statistical summary post-hoc t-tests between parents and non-parents

Population	*Period*	*t*	*df*	*p*
Migratory	October	-10.83	270.4	< 0.001
	November	-5.82	57.8	<0.001
	December- February	-4.19	80.5	<0.001
	March	-0.61	38.6	0.55
	April	-1.26	50.4	0.21
	May	-0.42	9.2	0.68
Non-migratory	October	-3.67	37.3	<0.001
	November	-0.55	51.6	0.58
	December- February	-1.33	41.7	0.19
	March	-1.70	70.6	0.09
	April	-0.70	81.2	0.48
	May	-1.44	31.8	0.16

Test results are from Welch t-test from package 'stats' in *R*.

The benefits of extended care are much less present in the non-migratory sub-population. The non-migratory sub-population does not experience the predation danger that the migratory sub-population does, making parental vigilance less beneficial. In the period prior and during migration, migratory geese have to store enough reserves to both successfully complete a 3000km migration and a costly period of breeding. On the contrary, non-migratory geese only have to prepare for breeding, whereas the competition for food is probably comparable because of the worse food conditions (Van der Jeugd et al. 2009).

An alternative hypothesis to explain the observed difference in parental care between the two sub-populations could lie in age structure. The non-migratory sub-population has a very high juvenile survival, and is growing almost exponentially. The migratory sub-population, on the contrary, has a much lower juvenile survival and is growing much more slowly (Van der Jeugd et al. 2009). As a result, the non-migratory sub-population probably consists of relatively more young individuals compared to the migratory sub-population. It may be that the parents observed in the migratory sub-populations are older than those in the non-migratory sub-population. For these older parents the expected future reproductive success will be lower than for the younger parents, resulting in longer parental care for the older parents. However, the difference in age structure should also cause differences in the vigilance behaviour of the non-parents, and our results do not show this.

Concluding, we show that differences in duration of parental care between migratory and non-migratory barnacle geese confirm the predictions of life-history theory with a drastic shorter parental care in the non-migratory population. To our knowledge, this is the first study that shows how being migratory or not affects the duration of parental care within the same species. These results are in line with our predictions and with predictions of many other studies. For example Klug and Bonsall (2010) show that parental care evolves under conditions where (among others) adult survival is relatively low and where the juvenile survival in the absence of care is low. Both conditions apply to the differences between migration and non-migration in our system. In African Buffalo *Syncerus caffer*, the population of Manyara continue to produce milk for offspring for 18 months, while those in the Serengeti stop producing milk after 10 months. Similar to our study the population with the longest period of care experienced the highest levels of predation danger (Prins 1996). However, good comparisons of parental investment between populations are scarce (and absent with respect to differences in migratory behaviour), despite the many theoretical predictions. Because we have compared two populations who only recently diverged, this provides great potential for understanding adaptive life-history evolution, as suggested by Keller and Taylor (2008).

Many migratory species are currently threatened by habitat fragmentation or global change (Wilcove and Wikelski 2008) and this is accompanied with species becoming less migratory or migrating over shorter distances (Visser et al. 2009; Pulido and Berthold 2010). From a theoretical point of view these changes are very interesting, as they may provide insights in the costs and benefits of migration. Our study provides an example of how such a change in migration can affect other behaviour, and illustrates that the migratory behaviour of individuals cannot be taken for granted when studying life-history trade-offs.

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Blood samples of barnacle geese from Spitsbergen, Russia and the Netherlands on ice

Chapter 5

The development of a genome wide SNP set for the Barnacle Goose

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Abstract

Migratory birds are of particular interest for population genetics because of the high connectivity between habitats and populations. A high degree of connectivity requires using many genetic markers to achieve the required statistical power, and a genome wide SNP set can fit this purpose. Here we present the development of a genome wide SNP set for the Barnacle Goose *Branta leucopsis*, a model species for the study of bird migration. We used the genome of a different waterfowl species, Mallard *Anas platyrhynchos*, as a reference to align Barnacle Goose second generation sequence reads from an RRL library and detected 2188 SNPs genome wide. Furthermore, we used chimeric flanking sequences, merged from both Mallard and Barnacle Goose DNA sequence information, to create primers for validation by genotyping. Validation with a 384 SNP genotyping set resulted in 374 (97%) successfully typed SNPs in the assay, of which 358 (96%) were polymorphic. Additionally, we validated our SNPs on relatively old (30 years) museum samples, which resulted in a success rate of at least 80%. This shows that museum samples could be used in standard SNP genotyping assays. Our study also shows that the genome of a related species can be used as reference to detect genome wide SNPs in birds, because genomes of birds are highly conserved. This is illustrated by the use of chimeric flanking sequences, which showed that the incorporation of flanking nucleotides from Mallard into Barnacle Goose sequences lead to equal genotyping performance when compared to flanking sequences solely composed of Barnacle Goose sequence.

Introduction

Migration of animals is one of the most visible natural phenomena and as such has attracted much scientific attention. Because migrants connect habitats, migratory species can play a key role in understanding how local environmental changes affect populations and habitats at a larger scale (Webster et al. 2002). Additionally, migratory birds, especially waterfowl such as geese and ducks, are thought to play an important role in the spread of infectious diseases such as Avian Influenza (Gilbert et al. 2006; Si et al. 2009). More insight into the genetic population structure of migratory species will be helpful in understanding migration patterns and possible migration changes (Wink 2006). Previous genetic studies on geese used microsatellites with varying success. For example, Anderholm et al. (2009) successfully showed nest parasitism in barnacle geese *Branta leucopsis* using 14 microsatellites, while Harrison et al. (2010b), using 15 microsatellite markers, could not discover population structure among 1127 light-bellied brent geese *Branta bernicla hrota*. However, because of the high connectivity between migratory populations, high discriminating power is needed to disentangle population structure, especially when insight in recent migratory changes is desired. The detection and development of Single Nucleotide Polymorphisms (SNPs) could fill this knowledge gap for migratory species since the statistical power of SNPs, of which hundreds can nowadays be easily applied in a single study, is considerably higher than of microsatellites (Morin et al. 2004; Morin et al. 2009). To our knowledge, for migratory birds only for the mallard (*Anas platyrhynchos*), which is a partial migrant, SNPs have been described genome wide (Kraus et al. 2011). The Barnacle Goose is one of the model species for migration research, studied especially for its flexibility in adjusting migration schedules to ecological changes (Larsson et al. 1988; Forslund and Larsson 1991; Filchagov and Leonovich 1992; Eichhorn et al. 2008; chapter two and chapter three). The Barnacle Goose has three different flyways (Madsen et al. 1999), which are assumed to have little exchange (Van Der Jeugd and Litvin 2006). Within the Russian flyway there are several populations, of which the Swedish and Dutch were established recently (Larsson et al. 1988; Meininger and Van Swelm 1994; Van der Jeugd et al. 2003). The development of large SNP sets makes it possible to analyse demography and recent development of new populations. Due to migratory changes problems occur such as increasing crop damage resulting in societal debate on whether conservation of geese is still needed or how crop damage can be reduced. Moreover, geese are important poultry species such as several varieties of Greylag Goose *Anser anser*. Although barnacle geese are not used in agricultural production, the detection of SNPs in Barnacle Goose may provide potential SNPs for related species and their domesticated forms.

Kerstens et al. (2009) and Van Bers et al. (2010) showed the efficient use of next generation sequencing for the detection of a large amount of SNPs without having a sequenced reference genome (in Turkey *Meleagris gallopavo* and Great Tit *Parus major* respectively). These studies created an incomplete genome from short sequences stemming from next generation Illumina sequencing and used that as a reference genome for SNP detection. The goal of our study was to detect SNPs in Barnacle Goose by using a reference genome from a different bird species, the Mallard (Huang et al. in prep), knowing that geese and ducks diverged approximately 30 million years ago (Hedges et al. 2006). The method presented can be of practical benefit for SNP detecting in other species.

Methods

Sample collection and preparation

The SNP discovery panel consisted of ethanol preserved whole blood samples from 16 individuals from Spitsbergen (Norway), The Netherlands and Russia (Table 5.1). We isolated DNA using the Gentra Systems Puregene DNA purification kit as described in

Table 5.1. Numbers of used individuals per location for the SNP discovery panel.

Population	*Coordinates (lat; long)*	*Number of individuals*
Spitsbergen – Nordenskioldkysten	77.8°; 13.6°	3
Spitsbergen - Ny-Ålesund	78.92°; 11.91°	4
Russia - Nova Zembla	71.4°; 54°	2
Russia – Kolguev	69.1°; 49.9°	2
Russia – Kanin	68°; 45°	2
The Netherlands - Krammersche Slikken	51.6°; 4.2°	3

(Kraus et al. 2011). We made two reduced representation libraries (RRLs) from a DNA pool of the discovery panel individuals with the restriction enzymes AluI and HaeIII. The RRL size ranged from 100 to 150 bp. We pooled equal amounts of the two RRLs and submitted them for sequencing on the Illumina GAII (Illumina Inc., USA) using the Illumina Sample Preparation protocols. Paired-end sequencing was performed for 101 cycles. For validation by genotyping we used the same individuals as those used for the discovery panel. In addition, we collected 26 samples from barnacle geese originating from Greenland and the wintering population in the Netherlands. We obtained the samples from pieces of flesh from the foot and we isolated DNA the same way as described above. Different from the blood samples, we repeated the Proteinase-K treatment several times because the tissue was very tough. As the tissue did not dissolve enough to allow Proteinase-K to work effectively, we further destructed the tissue by holding the tubes containing the samples in liquid nitrogen until they were completely frozen. Then, we took them out until they were completely thawed, and repeated this five times. Thereafter we had another few steps with Proteinase-K until the tissue was dissolved. We evaluated the DNA fragments of the museum samples for quality on agarose gels and measured quantity and purity on a Nanodrop ND-1000. We diluted all samples (16 from discovery panel and 10 from museum) to 50ng/µl for genotyping.

In silico SNP mining

Quality filtering of raw reads was carried out by Perl scripts. Due to the use of the restriction enzymes AluI and HaeIII all sequences should start with a cytosine (C). Sequences not starting with ‘C’ were therefore discarded from the dataset. We trimmed all reads beyond position 62, where the average phred quality score per base position (Ewing and Green 1998) dropped below 17. We treated sequence reads occurring in at least two identical copies in this subset as reliable, making quality checks for these specific reads unnecessary (Kerstens et al. 2009). We discarded any singleton sequence containing a nucleotide with a quality score of less than 15 as unreliable. Based on the raw sequence coverage of our RRLs (38X) we also excluded reads suspected to stem from repetitive regions by applying a fourfold overabundance threshold (Kerstens et al. 2009).

We aligned the resulting (quality filtered) reads to the reference genome with default parameters in MAQ (Li et al. 2008). Due to the lack of a sequenced goose genome we used Mallard genome scaffolds (Huang et al. in prep) as a reference. We considered only unambiguously mapped reads for SNP calling. Furthermore we filtered the candidate SNPs as predicted by MAQ according to the following criteria: minimal map quality per read: 10; minimal map quality of the best mapping read on a SNP position: 60; maximum read depth at the SNP position: four times the actual coverage after quality filtering; minimum consensus quality: 30. In addition we discarded SNP sites with a minor allele count of 1 or 2 as potential sequencing errors (Kerstens et al. 2009; Van Bers et al. 2010).

From the aligned Barnacle Goose reads we made a consensus file in MAQ to retrieve 50 bp flanking sequences of the SNPs on both sides. Whenever there were no flanking sequences available from the Barnacle Goose consensus, we used the flanking sequences obtained from the Mallard genome, resulting in a chimeric flanking sequence from both Mallard and Barnacle Goose. We retrieved all flanking sequences using ad hoc *R*-scripts (R Development Core Team, 2009). We used the amount of bases that originated from the Barnacle Goose consensus as a selection criterion for the 384 SNP genotyping set, because the genetic distance between Mallard and Barnacle Goose may be a cause of failure during genotyping, and hence we chose the SNPs with predominantly Barnacle Goose flanking sequences.

We mapped all SNPs against the Chicken *Gallus gallus* genome (Wallis et al. 2004) (WASHUC2) using Blastn (Altschul et al. 1997) with default settings. We used the Chicken genome, because it is the closest related species of which a physical genome map is available, thereby allowing us to predict the likely chromosomal position of the SNPs. Because of the high degree of conserved synteny between birds, this allows us to select evenly spaced SNPs in the Barnacle Goose, even in the absence of a Barnacle Goose genome sequence. As final selection criteria we used 1) the distribution of SNPs across the chicken genome to minimize physical linkage and dependence among the selected SNPs and 2) an Illumina assay design score of >0.8. Because of a higher recombination on the micro-chromosomes in birds we used a smaller SNP spacing for the micro-chromosomes (Table 5.2). Because we used a small number of individuals for the SNP detection we analyzed the frequency distribution of the minor allele frequencies (MAF) to assess the ascertainment bias. Additionally we calculated the transition/transversion ratios for the detected and selected SNPs.

Validation

For a pre-validation of our SNP detection approach we designed primers for a randomly chosen set of 25 SNPs using primer3 . All primers had annealing temperatures of 60°C. We made these primers based on flanking sequences obtained from (only) the Mallard genome reference sequence of 200 bp on both sides of each SNP. We picked eight individuals at random from the discovery panel for PCR amplification and Sanger sequencing. We screened the resulting sequences for the predicted SNPs with Gap4 of the Staden Package (Staden et al. 2000).

Table 5.2. Minimum distances between SNPs on the Chicken genome and the number of SNPs used in the 384 genotyping set per chromosome.

Chromosome	*Distance (kb)*	*Number of SNPs*
1	200	57
2	200	56
3	200	34
4	200	31
5	200	28
6	150	9
7	150	16
8	150	18
9	150	13
10	150	10
11	100	7
12	100	16
13	100	13
14	100	5
15	100	5
17	100	7
18	100	3
19	100	9
20	100	11
21	100	5
22	100	1
23	100	3
24	100	9
26	100	2
27	100	1
28	100	2
Z	200	12

For validation by genotyping we used all 16 individuals of the discovery panel, which were genotyped for 384 SNPs with the Illumina Golden Gate® genotyping assay on an Illumina® BeadXpress with VeraCode™ technology as described in Kraus et al. (Kraus et al. 2011). In contrast to the pre-validation, we based assay primers for each SNP on the chimeric flanking sequences. We performed the allele calling (clustering) with the program Genome Studio (Illumina). We calculated the observed MAF for each SNP with CoAncestry (Wang 2011) by taking the frequency of the least frequent allele and averaged that over all loci to obtain average MAF. In addition to the individuals of the discovery panel, we genotyped the 5 best museum samples originating from Greenland and the 5 best samples from wintering barnacle geese in The Netherlands. We selected those samples that had both sufficient amounts of DNA and of sufficient fragment lengths (sample codes: ZMA5090, ZMA5091, ZMA16572, ZMA17154, ZMA21106, ZMA27175, ZMA28449, ZMA28451, ZMA28453 and ZMA29205).

Results

We obtained 25.8 million reads of 101 bp length (2.6 billion nucleotides) using paired-end sequencing on two lanes of an Illumina GAII, representing approximately 5% of the genome with a estimated sequence depth of 38x (Figure 5.1, page 98). The raw sequencing data has been deposited in the NCBI sequence read archive (SRA) under accession number SRA029107. The number of 62 bp reads that passed the quality filters was 11 million (683.4 million nucleotides), providing a sequencing depth of 9.9x. We based these calculations on a 5% coverage, which may be an over-estimation because of the gaps in the middle of the larger RRL-fragments due to read trimming. Of these 11 million sequences 1.77 million (16.1%) aligned to the Mallard genome (Huang et al. in prep) which resulted in 363,014 candidate SNPs (mostly between Mallard and Barnacle Goose) as inferred by MAQ, of which 2188 SNPs (0.6%) passed all quality criteria. These SNPs have been deposited in the NCBI dbSNP database under accession numbers ss295471227 through ss295473414 for internal SNP identifiers Ble_1 - Ble_2188. We obtained 377 SNPs with at least 30 bp of goose consensus sequences on both sides of the SNP, 647 with 20-29 bp on both sides and 586 with 10-19 bp on both sides. The amount of SNPs detected per position on the reads was uniformly distributed (t= 1.06, d.f.= 2187, p= 0.29, Figure 5.2, page 98). The predicted mean minor allele frequency (MAF) of the 2188 SNPs, as inferred from sequencing the discovery panel RRLs, was 0.37 (Figure 5.3, page 98). A total of 923 SNPs could be mapped to unique locations distributed evenly over the Chicken genome (Figure 5.4, page 99). The transition/transversion ratio of all SNPs was 2.7.

Validation

Our pre-validation showed that, in eight individuals, 23 out of 30 (77%) primers of SNPs amplified in our PCR. Of these 23 we selected and purified PCR products of 16 primers, predicted to contain 25 SNPs. By sequencing the PCR products 19 out of 25 (76%) tested SNPs were ascertained in the sequencing results. The validation by genotyping, for which we used all 16 discovery panel individuals and the 10 museum samples, showed that 374 (97%) of the 384 assayed SNPs gave reliable genotypes in the assay and 358 (96% of the 374) were polymorphic. The quality of the historical samples was initially thought to be insufficient for SNP detection due to high fragmentation of the DNA. Of the initial 26 samples we used 10 samples, despite the agarose gel showing high degradation, for genotyping and our worst performing sample still had a success rate of 80% for the 374 SNPs. The lowest call rate among our discovery individuals was 91%. The heterozygosity of the genotyped discovery individuals was 0.34 and the measured mean observed MAF was 0.29. There was no effect of sequencing position in the read or origin of flanking sequence (proportion stemming from Barnacle Goose) on the technical failure of SNPs (position: $\chi2$= 59.1, d.f.= 63, p= 0.62; flanking origin: $\chi2$= 4.16, d.f.= 3, p: 0.25).

Discussion

This genome wide SNP development is, to our knowledge, the first for a fully migratory bird and the first in which a reference genome from another species was used. Previous genetic marker sets for goose species only included a small number of microsatellites (e.g.:Fowler et al. 2004; Fowler 2005; Anderholm et al. 2009; Harrison et al. 2010a; Harrison et al. 2010b), which have considerably less statistical power than the large number of SNPs we identified (Morin et al. 2009).

Despite using a relatively small discovery panel and limited read depth (< 10x), our distribution of MAF shows that also relatively low-frequency SNPs could be detected, which may be especially useful for discriminating populations. The transition/transversion ratio (TS/TV) of 2.7 for the detected SNPs is comparable to the TS/TV ratios described in other studies (Van Bers et al. 2010; Kraus et al. 2011). This high TS/TV ratio in general is a good measure for the low frequency of false positives in the SNP discovery analysis, which is also confirmed by our high SNP validation rate of 97 %. The quality variation in the first 5 positions of the sequence reads could be caused by a systematic sequencing error, which passed the quality filter because of the assumed low standard sequencing error rates of the Illumina GAII at the beginning of sequenced reads. Despite these irregularities, the validation rate of the SNPs selected from the first five was the same as for SNPs identified within other positions of the Illumina reads. This was probably caused by the selection criterion of the length of flanking sequences originating from Barnacle Goose. SNPs that were detected at the beginning or end of a known sequence were often not selected, because at least one flanking region had a low number of Barnacle Goose flanking bp. If they were selected, they had an overlap with other aligned reads, which reduces the chance of false positives. The selection of the 384 SNPs for genotyping did not result in a bias with respect to selected SNPs per position (Figure 5.2, in red, mean position selected, page 98) and predicted minor allele frequency (Figure 5.3, in red, page 98).

The museum samples that we genotyped performed with a minimum success rate of 80%. This provides opportunities for using relatively old highly degraded museum samples for SNP genotyping with the Illumina Golden Gate® genotyping assay, given that sufficient quantities of DNA are available. Caution should be taken however, as we selected those samples that we expected to have the largest chance of successful genotyping. We did not genotype all museum samples as it was not the main priority of our genotyping assays. Studies using only such museum samples should take potential loss of usable samples into account in the design. Still, earlier SNP genotyping of highly degraded DNA samples was tedious and only possible on low automation and throughput (Morin and McCarthy 2007).

Approximately 16% of our reads (that passed the quality filters) aligned to the Mallard genome. Because we obtained our SNPs from these reads, it is not surprising that also the nearby sequences from Mallard provided good flanking sequences for genotyping, because we apparently have a bias for SNPs in the better conserved regions of the genome. This extreme sequence conservation between the genera Anas and Branta, both belonging to the family Anatidae, corroborates earlier findings of highly conservative genome evolution in birds (Shetty et al. 1999).

Our results show that our method, in which we used the genome of the Mallard, provides excellently performing SNPs. We show that there is no effect on the performance of the SNP assay of the origin of flanking sequences in the assay design between these two species. Both SNPs with a high percentage of flanking sequences of Barnacle Goose and SNPs with a high percentage of flanking sequences of Mallard worked very well, and we observed no difference in their overall performance during genotyping. To our knowledge this is the first study in which chimeric flanking sequences are used successfully. We show that an RRL library can be used to obtain SNPs and flanking sequences by aligning to a related species of the focal species in birds.

With the current developments, sequencing costs are rapidly decreasing, which will make the use of RRLs redundant. However, in this study with an RRL approach we are able to demonstrate that our method could work equally well when scaled up to whole genome sequencing of a discovery panel of individuals using a reference genome of a related (bird) species. This makes the complicated steps of a de novo assembly for the focal species (Kerstens et al. 2009; Van Bers et al. 2010) obsolete for SNP detection aimed at medium sized SNP sets of a few hundred to a few thousand SNPs. Given our RRL size of 5% of the Barnacle Goose genome, and our 2188 detected SNPs therein, scaling up to a whole genome approach is expected to yield more than 43.000 SNPs.

This genome wide SNP development of the Barnacle Goose provides us with a tool to study the genetic effects of population, and possibly migration, changes within a species that is renown for its flexibility in migration (Eichhorn et al. 2008; chapter two and chapter three). The successful use of chimeric flanking sequences for genotyping our SNPs is in line with earlier findings and expectations for bird genome evolutionary patterns. Additionally, our study shows that the detection of thousands of assayable SNPs is now within reach for many more species than there is detailed genomic information for.

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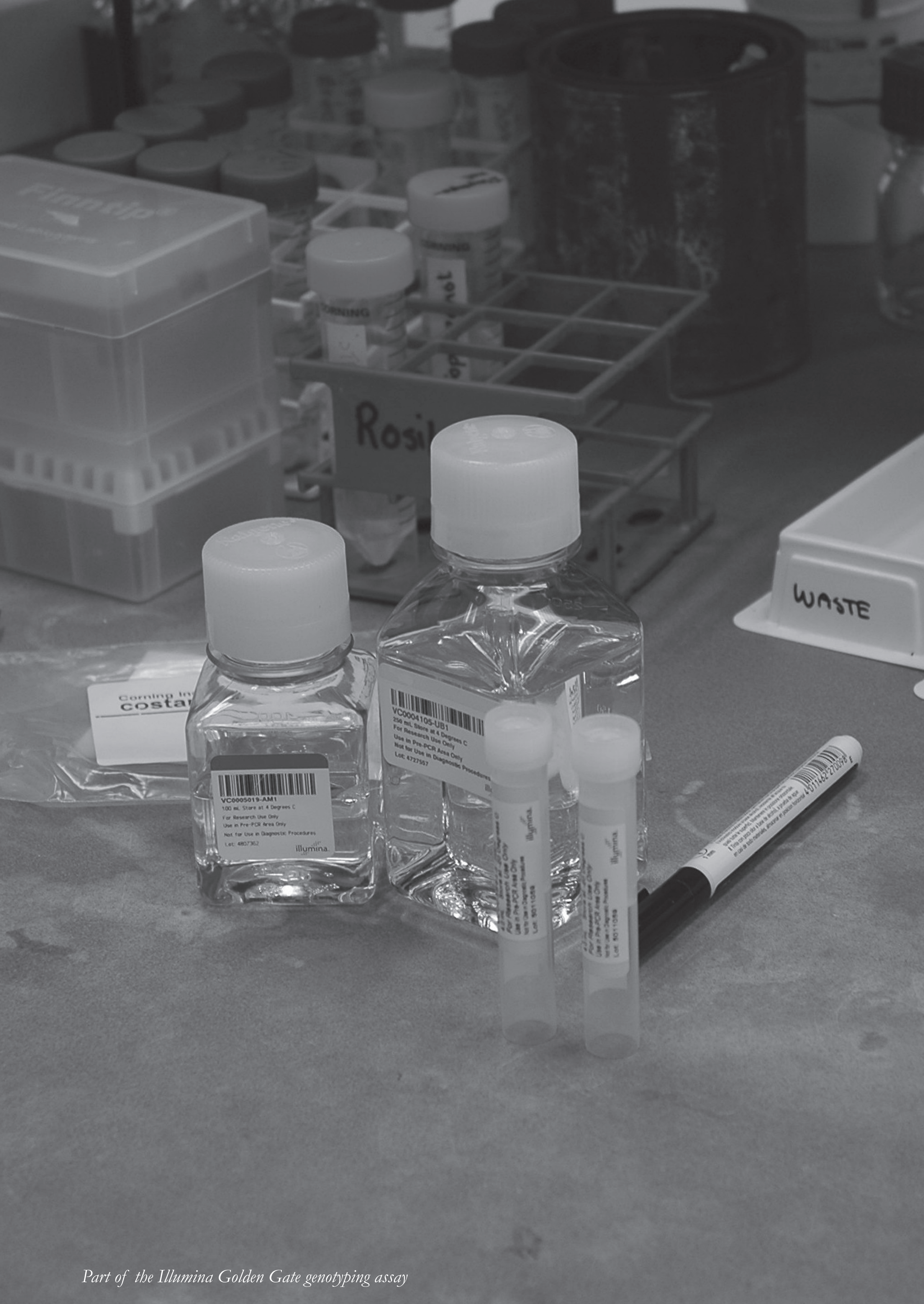

Part of the Illumina Golden Gate genotyping assay

Chapter 6

Genetic consequences of breaking migratory traditions in barnacle geese

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Abstract

Cultural transmission of migratory traditions is thought to increase separation between populations and consequently affect speciation. Recently, the migratory traditions of the Barnacle Goose *Branta leucopsis* have changed. Further, two new populations emerged. To explain these changes, one hypothesis suggests that the increasing population size of the Russian population reached the carrying capacity, leading to gradual expansion southward. An alternative hypothesis claims that a divergence in timing of spring migration and timing of termination of parental care reduced the cultural transmission of migratory traditions, with more exploratory individuals as a consequence.

Here, we studied the population genetic structure of the Barnacle Goose to test the validity of both hypotheses. We genotyped a set of 384 SNPs on 418 individuals from populations from Greenland, Spitsbergen, Russia, Sweden and the Netherlands. By calculating F-statistics we show that these populations are indeed differentiated. Despite the assumed traditions of migration within populations we also show that genetic exchange occurs between all populations. This result is supported by the presence of linkage disequilibrium in most populations, suggesting population admixture.

Hence, these results support the parental care hypothesis and suggest that changes in behaviour have caused colonization of new areas. Newly established populations are characterized by increased exploration, thereby increasing exchange between populations. These results suggest that use of migratory traditions is subject to change in geese and that such changes have population genetic consequences.

Introduction

Long distance seasonal migrations, in which individuals travel seasonally between a breeding and non-breeding range, often capture our imagination because of the large number of individuals that travel great distances every year. These individuals travel great distances, often much larger than their ranges during a specific season. This outstanding dispersal capacity of migratory species holds the potential of easily exchanging individuals between populations leading to high levels of gene flow. However, other aspects of behaviour, such as close family bonds reduce the amount of gene flow between populations. In geese, families are assumed to stay together for nearly a year and these close family bonds and cultural inheritance of migratory behaviour are assumed to have caused the closest kind of inbreeding present in arctic or subarctic birds, with the emergence of many different races as a result (Mayr 1942; Hochbaum 1955; Kear 1970; Baker 1978; Owen 1980). Recently, the migration system of the Barnacle Goose *Branta leucopsis* has gone through a number of striking changes. The Russian population has increased from 25,000 in the 1960s to 550,000 in 2006 and the Spitsbergen population increased from 3,000 in the 1960s to 30,000 in 2010 (Fox et al. 2010). Additionally, the barnacle geese migrating in spring from the Netherlands to Russia have delayed their commencement of migration by approximately one month since the 1970s. The cause of this delay is subject to debate as both competition for food (Eichhorn et al. 2008) and predation danger (chapter two) are suggested causes. Moreover, a new breeding colony has established on Gotland, Sweden in the 1970s (Larsson et al. 1988) and in the southwest of the Netherlands in the 1980s (Meininger and Van Swelm 1994). The populations breeding in Russia, Sweden and the Netherlands winter in the Netherlands. Recently, also the population breeding on Spitsbergen started to delay the commencement of spring migration (Outman et al. unpublished data).

It has been suggested that the range expansion, from breeding only in Russia to breeding in the Baltic and the Netherlands, is merely a result of increased dispersal and exploration by individuals belonging to the rapidly growing Russian population as a reaction towards increased competition for food and space, combined with improved feeding conditions further south due to changes in agricultural practice (Van der Graaf et al. 2006a; Van der Jeugd et al. 2009). As a consequence of increasing population size, food competition increased at breeding sites and forced geese to gradually colonize new breeding sites more south. We will refer to this as the *food competition hypothesis*. However, this is not in line with the traditions of migration in geese. Obviously, these migrants with learned migratory traditions are more flexible than migrants in which their destination or route is genetically programmed (Sutherland 1988; Sutherland 1998). However, some mechanism of breaking of such traditions is mandatory for a change in migration to emerge. One possible mechanism is that the traditions are not successfully transmitted to the next generation. For instance, the delay in migration, and the observed shortening of parental care of the barnacle geese migrating to Russia (chapter three) caused a gap of 2 months between the end of parental care and the commencement of spring migration. As juvenile geese are known to become more explorative after leaving the family (Baker 1978), such a gap could lead to increased exploration and hence accelerate colonization of new breeding sites. We will refer to this as the *parental care hypothesis*.

Here we studied the population genetic structure of the Barnacle Goose to test the different hypotheses on the cause of the colonization of the different populations. Both the food competition hypothesis and the parental care hypothesis may result in different population genetic structure. In the food competition hypothesis a gradual colonization from Russia to Sweden to the Netherlands would predict that the Swedish population is genetically intermediate between the Russian and the Dutch population, and the consequent gene flow would be high from Russia to Sweden and from Sweden to the Netherlands. Competition for food in the Russian Arctic, and as a result individuals leaving that population, would also predict higher emigration rates than immigration rates for Russia. In the parental care hypothesis we expect more gene flow from Russia to the Netherlands than from Sweden to the Netherlands. In addition to gaining insight in the colonization history of the new populations, we also include the Spitsbergen and Greenland populations in our analysis to understand the population genetics of the Barnacle Goose at a global scale and shed light on the evolution of the migration system of the Barnacle Goose.

Methods

Study Populations and Sampling

We used previously collected samples of the five main populations of the Barnacle Goose: Greenland (GL), Spitsbergen (SP), Russia (RU), Sweden (SE) and the Netherlands (NL). These populations represent three different flyways: The Greenland and Spitsbergen populations use separate flyways and have non-overlapping winter ranges, whereas the Russian population and the newly established populations from the Baltic and the Netherlands share a flyway and have winter ranges that largely overlap (Figure 6.1, page 102). For Greenland, only tissue samples, obtained of the foot sole and originating from the 1970s, from the collection of the Zoological Museum Amsterdam were used. From all other populations we used ethanol preserved whole blood samples. We isolated DNA using Proteinase-K and the Gentra Systems Puregene DNA purification kit as presented in chapter five. Samples from Spitsbergen were collected in 2007 from the colonies near Nordenskioldkysten, Ny-Ålesund and Longyearbyen. Russian samples originated from the colony of the Kolokolkova Bay near Tobseda (Van der Jeugd et al. 2003) and were collected in 2007 and 2008. Swedish samples were collected from the Gotland population (Larsson et al. 1988) between 2002 and 2006. Samples from the Netherlands were collected in the Krammersche Slikken in 2007 and 2008. For an overview of locations and sample size per population see Table 6.1. All samples were collected conform to national and institutional rules. It has to be noted that the collected samples represent a cross section from these populations covering a time period around roughly one decade before the moment of sampling, as most individuals were adults and barnacle geese have an average life expectancy of 8 to 15 years (depending on population).

Table 6.1. Overview of origin of individuals.

Location	*Lat/lon*	*Number of individuals*
Greenland	70.4° N / 22.3° W	5
Spitsbergen	78° N / 12° E	117
Russia	70° N / 50° E	107
Sweden	57.27° N / 18.45° E	55
The Netherlands	51.6° N / 4.2° E	134

We used the Illumina Golden Gate® genotyping assay on an Illumina® BeadXpress with VeraCode™ technology to genotype each individual for 384 Single Nucleotide Polymorphisms (SNP) presented in chapter five and the program Genome Studio (Illumina) for allele calling (clustering) for each SNP individually.

General Population Genetic Analyses

We tested all SNP markers for deviation from Hardy-Weinberg equilibrium (HWE) within all populations using the package Adegenet 1.2-8 (Jombart 2008) in *R* (*R* Development Core Team, 2009). We calculated pairwise F_{ST} for all populations with the program Arlequin 3.5 (Excoffier and Lischer 2010) and tested the significance of these observed F_{ST} values by a permutation procedure using 10.000 permutations, thereby creating a panmixia, and testing the observed allele frequencies against the permutated.

Discriminant Analysis of Principal Components

We used Discriminant Analysis of Principal Components (DAPC) (Jombart et al. 2010) to detect the population structure. This method identifies genetic clusters and unravels complex population structures. We used the percentage of successful assignment as a measure of group differentiation, corrected for the number of retained principal components (function a.score). In this procedure each individual was first assigned to the population from which it was sampled (prior population), and then assigned to the population (of all the prior populations) that fits best. When the prior and assigned population are the same, high probabilities of assignment to the prior population are obtained. Because using too many principal components leads to overfitting of the model, the successful assignment is corrected for the number of principal components. We chose the optimal number of retained principal components using the function optim.a.score (with 20 simulations per principal component). In our study we retained 50 principal components cumulatively explaining 45 % of the variance.

We ran two DAPC analyses. First we assigned each individual a priori to its population of origin (a priori population assignment), and obtained for each individual the probability of assignment to their populations of sampling. This allowed us to test which of the prior populations an individual could be assigned to best, and showed us whether individuals recently moved from one population to another. Thereafter, we used the find.clusters function, to ascertain the number of clusters and assign each individual to a cluster without providing any a priori population assignment. As for the a priori population assignment we obtained a probability of assignment to each cluster for each individual a posteriori (a posteriori population assignment). This removes the effect of assigning populations a priori on the eventual assignment to clusters and offers an unbiased interpretation of population structure.

Linkage Disequilibrium

We used CoAncestry (Wang 2011), with standard settings unless mentioned differently, to calculate relatedness between all individuals in our dataset. Of pairs that had a relatedness higher than 0.2 we removed one individual in order to remove possible family substructure present in the data set. With this new dataset we tested for each pair of SNPs whether there was significant linkage disequilibrium. We used the method LD from the *R*-package Genetics (Warner and Leisch 2002). Only those markers polymorphic within each population were tested. Bonferroni correction for multiple pairwise comparisons thus resulted in a different p-value threshold per population because in some populations more SNPs were polymorphic than in others.

Gene Flow Model Selection

We used the program Migrate-n (Beerli 2009) to compare different models of gene flow among the populations. By comparing such models we can test hypotheses on the evolution of migratory flyways of the Barnacle Goose, and we can test hypotheses on the origin of the non-migratory population in the Netherlands. In these analyses samples from Greenland were not used because they were collected before the Swedish and Dutch populations emerged, which makes inference of gene flow between these populations from present day data dubious.

We defined seven candidate models constraining the presence and directionality of migration between the four populations: Spitsbergen, Russia, Sweden and the Netherlands. Model 1 allowed gene flow between all possible populations pairs. In the more specific models we defined, for example, that there could be no gene flow between populations pairs, or that gene flow may be unidirectional in some cases. In model 2 there was no gene flow between Spitsbergen and any other population, except to and from the Netherlands. Between Russia, Sweden and the Netherlands two-way gene flow was possible. Model 3 was very similar to model 2, with the difference that it does not allow gene flow from Spitsbergen to the Netherlands. Model 4 reflects the situation before the emergence of the additional populations in the 1970s. At that time, only the Russian and Spitsbergen (and Greenland) population were present, which are assumed to have had some exchange. From the Russian population the Swedish and Dutch emerged, reflected in our model by allowing gene flow between these populations. Model 5 is different from model 4 in that there is no direct gene flow from Russia to the Netherlands. This model represents the situation that there is gene flow between Russia and Sweden, and between Sweden and the Netherlands, and that the colonization of the Netherlands took place via the Swedish population. This model reflects a gradual expansion of the breeding range of the Barnacle Goose with increasing population size. Model 6 reflects colonization of the Netherlands and Sweden from Russia, without allowing any gene flow between Sweden and the Netherlands. In model 7 one-way gene flow from the

Netherlands to Sweden is added to those possible in model 6. This model is based on the hypothesis of more explorative Dutch geese migrating to Sweden, but not the other way around. See Table 6.4, column *model parameters*, for a summary.

We compared the models using Bayes Factors (Beerli and Palczewski 2010), which are marginal likelihoods over the complete parameter range (Newton and Raftery 1994). We ranked the Bayes Factors of all models where model 1 was the model with the highest harmonic mean (HM) of the marginal likelihood This difference between two harmonic means is denoted as dHM. We calculated the probability of each model using the method explained in Beerli and Palczewski (2010).

Results

The number of polymorphic SNPs for the entire sample (all populations combined) was 358. In the Greenland samples were 282 polymorphic SNPs, whereas the other populations all had more than 350 polymorphic SNPs. The vast majority of our SNPs was in Hardy-Weinberg equilibrium (GL: 100%, SP: 96%, RU: 95%, SV: 98%, NL: 95%, $\alpha=0.05$). Calculation of pairwise F_{ST} values show that there is significant population structure. Although the F_{ST} values are very low, all F_{ST} are significantly different from 0 (Table 6.2). The number of samples from Greenland was very low, so the F_{ST} values between Greenland and the other populations should be interpreted with caution. The F_{ST} analyses show that Greenland is most separated from the other populations with values ranging from 0.032 to 0.038. The Spitsbergen population is least differentiated from the Russian population (F_{ST}: 0.020) and approximately equally differentiated from the Swedish and Dutch population (F_{ST} respectively 0.026 and 0.027). The Swedish population and the Russian population are the two least differentiated populations with an F_{ST} of 0.006. The F_{ST} values from the Dutch population indicate that the Russian and Dutch populations are less differentiated (F_{ST}: 0.015) than the Dutch and Swedish populations (F_{ST}: 0.018).

Table 6.2. F_{ST} values between each population.

	Greenland	Spitsbergen	Russia	Sweden	Netherlands
Greenland	*				
Spitsbergen	0.032	*			
Russia	0.033	0.020	*		
Sweden	0.038	0.026	0.006	*	
Netherlands	0.038	0.027	0.015	0.018	*

All calculated F_{ST} values were significant at the P<0.0001 threshold.

Discriminant Analysis of Principal Components

The DAPC analysis, while retaining 50 principal components explaining approximately

45% of the variance in our data of prior clusters, confirms the presence of the genetic structure as indicated by the F_{ST} analysis. Both the F_{ST} values and the PCA plot indicate that Spitsbergen is relatively differentiated from the other populations. Furthermore, these results show that Sweden and Russia are closer to each other than to the Dutch cluster (Figure 6.2a, page 102). The probability of assignment of individuals to their original sampling locality (Figure 6.3a, page 106) shows that the individuals from Greenland were all assigned to the Greenland clusters with probabilities close to 1. For Spitsbergen, most individuals were assigned to the Spitsbergen cluster, but some individuals had a high probability of being assigned to the Russian genetic clusters, and some have a probability of being assigned to the Dutch, and to a lesser extent to the Swedish cluster. In the Russian population most individuals had the highest probability of being assigned to the Russian cluster, but a large proportion of individuals show a substantial probability of assignment to the Dutch and Swedish clusters. The results for the Swedish population shows that approximately half of the individuals were assigned to the Russian and half to the Swedish cluster. Only few Swedish individuals had high probabilities of assignment to the Dutch cluster. Of the Dutch population most individuals were assigned with high probabilities to the Dutch cluster and a small number of individuals had high assignment probabilities to the Russian cluster. Only very few individuals had some assignment probability (between 0 and 0.3) to the Swedish genetic cluster.

The DAPC analysis without assigning individuals to populations a priori (Figure 6.2b, page 102 and Figure 6.3b, page 106) shows that most individuals of the Spitsbergen population were assigned to the same cluster (cluster 2). The individuals of the Russian and Swedish population were assigned mostly to the same cluster (cluster 1). Cluster 6 consists of individuals originating from Spitsbergen, Russia, Sweden and the Netherlands. Most individuals from the Netherlands are assigned to clusters 3, 4 and 5. These clusters contain (except for one Swedish individual) no individuals from other populations than the Dutch population.

Linkage Disequilibrium

We detected linkage disequilibrium between SNPs in all but the Greenland population. In the Spitsbergen population 63 pairs of SNPs (0.05%) showed linkage disequilibrium. Also in the Russian population (40 pairs, 0.03%), the Swedish population (33 pairs, 0.03%) and the Dutch population (130 pairs, 0.10%) many SNP pairs were in linkage disequilibrium (Table 6.3).

Migration rate model comparison

Our comparison of candidate models of gene flow between populations showed that the full gene flow model (Model 1) fitted our data best (Table 6.4). The large difference in harmonic mean of the marginal likelihood between the models results in a probability of 1 ($-0.1\cdot10^{-27}$) for this model. Thus, we further only report results for model 1. In analysis with Migrate-n gene flow outputs are scaled to mutation rate, and because we do not know the mutation rate of our SNPs, but assume that this is equal for all populations, the estimated gene flow is presented as relative measures. For convenience we scaled all gene flow measures relative to the smallest, which is SE→SP. For example, we can conclude that the mode of the estimated gene flow from Spitsbergen to Sweden (SP→SE) is 2.03 times larger than from Sweden to Spitsbergen. A number of patterns become clear from these gene flow measures (Figure 6.4a and Figure 6.4b, page 103). The gene flow measures to Sweden (SP→SE, RU→SE, NL→SE) are all relatively high (average: 2.08), whereas the gene flow measures from Sweden are relatively low (average: 1.17). For the Netherlands, the pattern is the opposite. The gene flow measures to the Netherlands (SP→NL, RU→NL, SE→NL) are relatively low (average: 1.30), whereas the gene flow measures from the Netherlands are relatively high (average: 1.93). The gene flow measures from Spitsbergen (SP→RU, SP→SE, SP→NL) is relatively higher (average: 1.75) than gene flow measures to Spitsbergen (average: 1.43). Finally, the gene flow measures from Russia (RU→SP, RU→SE, RU→NL) are similar (average 1.53) to the gene flow measures to Russia (average: 1.57).

Table 6.3. Number of pairs of markers in linkage disequilibrium (LD) and associated p-value thresholds (0.05/((n*n-1)/2)) for LD.

	Nr of pairs in LD	*P-value threshold*	*n (SNPs)*	*# of individuals*
Greenland	0	$1.262\cdot10^{-06}$	282	5
Spitsbergen	63	$8.048\cdot10^{-07}$	353	112
Russia	40	$8.002\cdot10^{-07}$	354	103
Sweden	33	$8.140\cdot10^{-07}$	351	49
Netherlands	130	$8.094\cdot10^{-07}$	351	79

The number of polymorphic SNPs in each population is n. The number of individuals is the number that remained in the analysis after removing the closely related individuals.

Discussion

The presence of significant F_{ST} values shows that the global population of the Barnacle Goose is not in panmixia. The selected populations from Greenland, Spitsbergen, Russia, Sweden and the Netherlands are distinct genetic populations, although closely connected. This is supported by the DAPC. We can conclude that the Greenland population is relatively isolated, although the small number of individuals from this population requires some reservation for this conclusion. This becomes especially clear when inspecting the position of the Greenland population in the structure in Figure 6.2b (page 102), which is somewhat in between all the other populations and is thus inconsistent.

The genetic distance between the Spitsbergen population and the Russian, Swedish and Dutch population is larger than among the last three populations, with the Russian population being closest, which shows that the Swedish and Dutch population recently diverged from the Russian and that the Swedish individuals did not play a major role in colonizing the Netherlands as breeding area. The DAPC results with populations assigned a priori show this same pattern, but also show that the Swedish population and the Dutch population seem to diverge from the Russian into different directions, suggesting that they both originate from the Russian population. This is in contrast to what we expected for the food competition hypothesis, namely that the Swedish population would have been intermediate between the Russian and Dutch population.

Table 6.4. Bayes Factors model comparison of migration models.

Model	*Model parameters*	*harmonic mean (HM)*	*dHM*	*Probability*
Model1	**** **** **** ****	-5899	0	1
Model2	*00* 0*** 0*** ****	-7428	-1530	0
Model3	*00* 0*** 0*** 0***	-6537	-639	0
Model4	**00 **** 0*** 0***	-7076	-1177	0
Model5	**00 ***0 0*** 00**	-8178	-2279	0
Model6	**00 **** 0**0 0*0*	-8191	-2293	0
Model7	**00 **** 0*** 0*0*	-7819	-1920	0

In this model comparison four populations were used: 1) Spitsbergen, 2) Russia, 3) Sweden, 4) The Netherlands. Model parameters code as follows: the first four signs indicate migration to the 1st population from population 1, 2, 3 & 4. The second four signs indicate migration to the 2nd population from 1,2,3 & 4. The 1st sign of the 1st quartet and the 2nd of the 2nd quartet indicate estimation of theta for population 1, 2 etc. An asterisk indicates that that particular migration rate was estimated by the model, a 0 indicates that no migration was allowed. For example, for model 2: no migration from Russia and Sweden to Spitsbergen was estimated, and no migration from Spitsbergen to Russia and Sweden was estimated. For each model we used 4 heated chains with 1, 1.5, 3, 1000000 heating scheme. The sampling increment in the prior was set to 20, the number of steps discarded (burn-in) was 2.000.000, and the number of steps analysed was 5.000. Prior theta's were generated from a uniform distribution ranging from 0 to 15, and prior migration rates were generated from a uniform distribution ranging from 0 to 4000.

Population assignment with prior population definitions using DAPC indicates that some individuals in the Spitsbergen, Russia, Sweden and the Netherlands populations had a significant probability of being assigned to another population than a priori defined. This suggests recent migration of individuals from the other populations to the population in which they were sampled. That this happens with a large proportion of individuals suggests that many individuals are currently migrating between the populations, very unlike the suggested traditions in geese (Mayr 1942; Anderson et al. 1992). This admixture, i.e., recent mixing of previously separated populations, is supported by the linkage disequilibrium between SNPs found in all (except Greenland) populations, because admixture is the most likely cause of linkage disequilibrium (Hartl and Clark 2007). This admixture contradicts the concept of migratory traditions or at least suggests that these traditions have broken.

The posterior cluster analysis indicates that Spitsbergen is a separate cluster, and that most individuals from Spitsbergen are also a posteriori assigned to this cluster. Most of the individuals from the Russian and Swedish population are assigned the same cluster, indicating that these two populations are much more connected to each other than to other populations. During wintering in the Netherlands individuals from the Russian and Swedish population mainly reside in the north of the Netherlands, while the individuals from the Dutch population mainly reside in the south as indicated from the ring recoveries discussed in chapter four. This could explain the strong connection between the Swedish and Russian population. The Netherlands shows substructure, resulting in three separate clusters, which are very distinct for the Netherlands. This could for example be caused by founder effects of recent colonization. There is no distinct Greenland cluster, which is most likely caused by the small sample size of that population.

Our estimated migration rates to and from all populations show a number of striking points. The Netherlands has on average the highest emigration, and the lowest immigration rates (Figure 6.4, page 106). Potentially, the difference in seasonally migratory behaviour of the Dutch population as compared to all the others (the Dutch population is the only non-migratory population) reduces the chance of settling permanently in the Dutch population, as adults who already adopted a migratory life style from their traditions may not be likely to lose that. However, individuals from the Dutch populations frequently emigrate to other populations, and more to Sweden and Spitsbergen than to the Russian population. The high emigration rate could be caused by the very short duration of parental care in the non-migratory Dutch population (chapter four). Whereas parents in the (migratory) Russian population provide parental care until approximately early March, the parents in the (non-migratory) Dutch population provide parental care only until the end of November. As juveniles are suggested to venture on exploratory trips after being released from the family (Baker 1978), this increases the exploratory potential for the Dutch population. This suddenly increased exploration has the effect that previously separated populations start to mix, causing admixture. Because admixture disappears very rapidly, our results suggest that this mixing did not start longer than a few generations ago, which fits the time scale of the behavioural changes in migration and parental care duration presented in chapter two and three.

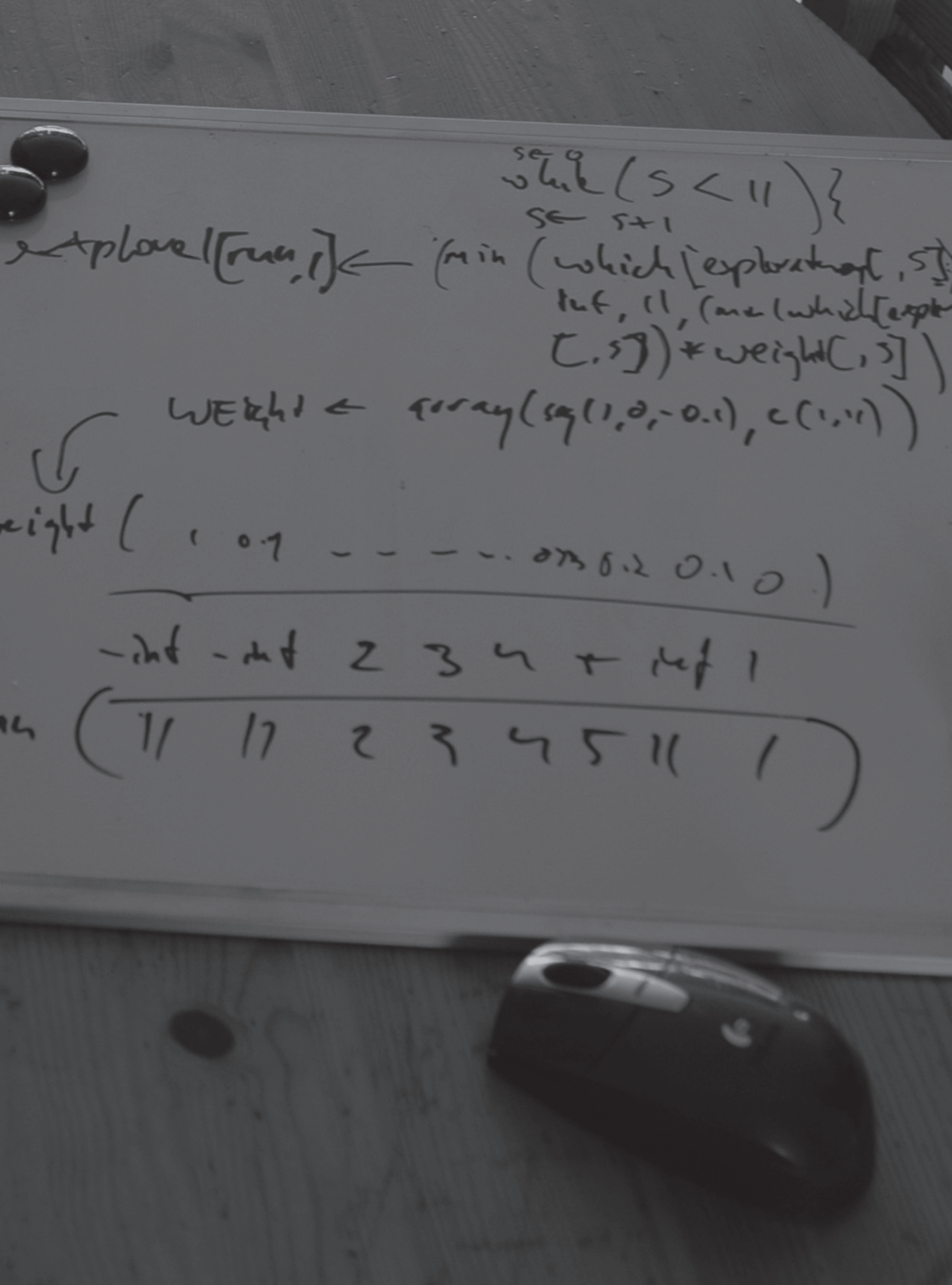
Another striking result from the gene flow estimation is that Sweden has much more immigration than emigration. Perhaps this is caused by increased predation in the Baltic by birds of prey and foxes (chapter two; unpublished data K. Larsson), but it is also suggested that the growing population in the Baltic has reached its carrying capacity (Eichhorn et al. 2008). Bearing in mind that most sampled individuals were individuals born in the 1990s and 2000s, this is in line with the observation that the rapid increase of the Baltic population during those years could only be explained by a net immigration of, most probably, Russian individuals (Larsson et al. 1988). The emigration rates for the Spitsbergen population are much larger than the immigration rates. Together with the strong population increase (Fox et al. 2010) this points at high productivity in this population, and it is possible that this has led to a carrying capacity problem here. The Russian population shows approximately equal immigration and emigration rates, suggesting that there is no carrying capacity problem, despite an also rapidly growing population (Fox et al. 2010). This difference between Spitsbergen and Russia could lie in the geography of both populations, as Spitsbergen is an archipelago without much room for gradual expansion in the arctic because most of its interior is not suited for geese.

Other studies have estimated exchange of individuals based on resightings of marked individuals. They found that exchange occurred among all populations, except between Greenland and Russia/Baltic/Netherlands. Exchange was relatively common between Greenland and Spitsbergen (Black 2007) and emigration from Sweden to both Russia and the Netherlands was more common than from Sweden to Spitsbergen (Van Der Jeugd and Litvin 2006). Black reported that exchange was frequently reported in adult birds that most likely returned to their original population, while van der Jeugd & Litvin documented natal dispersal and concluded that permanent emigration and breeding was likely in most cases (and definitely proven in at least three birds). Unpublished recent results indicate that permanent emigration from the Netherlands to Russia is especially common, with several cases of Dutch born birds breeding in two Russian study areas (Anisimov, Litvin & van der Jeugd, unpublished results). However, observations of individuals in populations other than their natal populations does not necessarily mean that there is also gene flow between these populations, and comparison of their estimates with our results is thus difficult.We are aware of the fact that we did not include Greenland in the migration rate analysis, whereas the Greenland population may play a role in these observed migration rates. However, it is assumed to be the most distant population and as long as migration rates from unsampled populations are not huge, migration rate estimation is suggested to be fairly robust (Beerli 2004).

We conclude that a capacity problem in the Russian arctic, and the consequent food competition hypothesis, would have resulted in a different genetic pattern than we observe here. Higher emigration rates for the Russian population would have been expected. Also, because this hypothesis suggests a gradual expansion of breeding range, a stronger connection between the Swedish and Dutch population would have been expected. The strong emigration from the Netherlands suggests increased exploration by Dutch barnacle geese, which supports the parental care hypothesis. Because the Dutch population is still growing rapidly, the survival of juveniles after fledgling is 0.97 during the first year and the virtual absence of predators in the Netherlands, capacity problems in the Netherlands cannot explain this high emigration. Another support for this hypothesis is the admixture in the Spitsbergen, Russian, Swedish and especially the Dutch population, which suggests recent mixing of populations that were separated previously.

An important aspect in understanding the migration between populations is the pair formation in winter. As the individuals from the Russian, Swedish and Dutch population winter in the Netherlands, there is considerable potential for exchange between these populations. Barnacle geese are known to have a preference to mate with individuals that are familiar from earlier in life (Choudhury and Black 1994). Thus, although pairs between individuals from the same population will be most common, pair formation with unfamiliar mates can occur, and when populations are mixed during winter, inter-population pairs can be formed. Because of the strong female philopatry in geese (Van der Jeugd et al. 2002), a male from another population will join its new mate to her population. Although this can play a role in migration between existing populations, it cannot explain the sudden colonization of populations and the increased exploration by Dutch individuals. It would be very interesting to test this sex specific migration in future studies.

Some studies (Anderson et al. 1992; Fowler et al. 2004) suggested that because of the strong traditions in geese, populations become separated despite relatively close proximity. The amount of migration shown by our results at least shows that this is no longer the case for the Barnacle Goose. However, we feel that other studies may have missed to draw similar conclusions because they assumed the traditional migration mechanism. A nice example is the study of Harrision et al. (2010b), who studied light-bellied brent geese *Branta bernicla hrota* in Ireland and assume that cultural transmission of migration and consequent site fidelity should cause isolation between populations with the consequent genetic effects. They do not find genetic differentiation between population, but still conclude that cultural inheritance drives site-fidelity. As they also found that nine pairs of loci of their sample showed evidence of linkage disequilibrium (Harrison et al. 2010a), they potentially found that for that species traditions are changing resulting in mixing of populations, but they did not conclude that. Our study shows that this mechanism cannot be taken for granted any longer in geese, and that changes in the traditions of migrations can have large effects on population genetic structure.



```
seq
while(s < 11){
s<- s+1
explore1[run,1] <- (min(which[exploration[,s]
inf, 11, (min(which[explo
[,s])) * weight[,s] )
WEight <- array(seq(1,0,-0.1), c(1,11))

eight ( 1 0.9 - - - - - . 0.3 0.2 0.1 0 )
-inf -inf 2 3 4 + inf 1
n ( 11 11 2 3 4 5 11 1 )
```

Programming in progress...

Chapter 7

Synthesis

Rudy M. Jonker

Understanding migratory behaviour

The central theme of this thesis is to understand changes in migratory behaviour of the Barnacle Goose and the role of parental care in this process. In **chapter two** I studied the possible factors of a migratory delay of one month. I showed that both increased predation danger and increased competition for food in the Baltic stopover are potential causes of this delay. Thereafter, in **chapter three** I studied whether this delay affected the duration of parental care in migratory barnacle geese. Barnacle geese did not delay the termination of parental care, as we expected, but advanced this date, which led to a gap of two months between the end of care and the commencement of migration. In **chapter four** I compared the duration of parental care of the migratory population with the (Dutch) non-migratory population. I show that this non-migratory population provides even less care as they terminate care in the end of November or early December, whereas the migratory population provided care until March. In **chapter five** I presented a 384 SNP set and in **chapter six** I used it to study the population genetic structure of the global Barnacle Goose population. From the population genetic structure I concluded that the populations of barnacle geese mix more than they used to and that increased explorative behaviour undermines the mechanism of cultural inheritance of migratory behaviour, with consequent high migration rates between all populations. In this synthesis I will discuss how these results relate to each other and what new perspectives they bring. For this I use the four questions of Tinbergen (Tinbergen 1963).

1. **Function.** Can we explain the delay of migration from a functional perspective? Can we use life-history theory to distinguish between competition and predation as factors affecting the delayed migration in barnacle geese?
2. **Phylogeny.** What is the phylogenetic background of the long duration of parental care in geese? What are the potential effects of shortening parental care and consequent increased exploratory behaviour on speciation?
3. **Causation.** What is the role of cultural transmission of migratory behaviour on the emergence of new migratory behaviour? Does the gap between the end of parental care and beginning of spring migration explain the migratory changes? And related to this:
4. **Ontogeny.** How does an individual acquire migratory behaviour?

1) Functional view on migratory change

In **chapter two** I discussed the possible explanations for the one month delay in commencement of spring migration in barnacle geese, that has been observed between the 1970s and the 2000s. For this I used a dynamic programming approach. The logic of this method is that there is some predefined goal that an individual has to reach: maximum fitness defined by the terminal reward function. In the case of barnacle geese this terminal reward is dependent on the amount of energy reserves and the time of arrival at the breeding area in the arctic. The model then calculated what the individual could do to maximize that reward. The resulting behaviour is the behaviour that maximizes life time reproductive success for that given environment. I showed that the observed change would not be adaptive when the sole cause of the change was climate change; with the known increase of spring temperatures in the flyway of barnacle geese an advancement instead of a delay of migration would be adaptive. The two remaining hypotheses: 1) increased population size resulted in increased competition for food on stopover sites and, 2) increased predation danger caused by the recovery of avian predators on the stopover sites, both suggested a delay in migration to be the adaptive response to the described change.

In **chapter three** I have studied the duration of parental care in migratory barnacle geese. I compared new observations with assumed duration of parental care from the 1980s. Based on these observations, I concluded that the duration of parental care shortened with at least one month. This change in behaviour has consequences for the cultural transmission of migratory behaviour, which I will discuss later in this synthesis. Furthermore this observation can be interpreted as indicator of environmental quality and population change when seen in the context of optimality theory (Rosenzweig 2007). In **chapter four**, I provided the tool, a model, that allows comparison between populations with respect to parental care and how this parental care is affected by the current and the expected future reproductive success. In this model, there is a simple trade-off between investment in current (*CRS*) and future (*FRS*) reproductive success, the sum of which is equal to lifetime (*LRS*) reproductive success. The model is based on the assumptions that individuals behave in such a way that they maximize life time reproductive success, assuming that the duration of parental care is a good approximation for the investment in current reproductive success. The assumed costs and benefits of parental care are such that the marginal benefit declines with increasing duration of parental care, while the marginal cost increases with the duration of parental care (Figure 7.1), and the steepness of these cost and benefit curves are determined by the second derivative R_{mb} (benefits) and R_{mc} (costs), which are explained in more detail in **chapter four**. The optimal duration of parental care I^* is given by

$$I^* = \frac{R_{mb}}{R_{mc} + R_{mb}} \quad \textit{eqn.}\ 7.1$$

If we assume that the situation before the delay is the situation depicted in Figure 7.1, we can reason how hypotheses for the delay of migration would affect parental investment. Scenarios in which either there is more competition for food or in which there is more predation danger both affect the *FRS* and the *CRS*, as adult survival, offspring survival and the preparation for breeding will all be affected. This effect is ΔR_{mc} for *FRS* and ΔR_{mb} for *CRS*.

A reduction of parental care is adaptive when $\Delta R_{mc} < \Delta R_{mb}$ (please note: positive effects of environmental change have a $\Delta<0$, whereas negative effects have a $\Delta>0$). For example, when the R_{mb} decreases with 20% and the R_{mc} decreases with 10% as a result of increased food competition or increased predation danger, I^* decreases with 6%, whereas when R_{mb} decreases with 10% and the R_{mc} decreases with 20%, I^* would increase with 6%. Figure 7.2 shows these examples graphically. The grey lines represent a changed environment in which R_{mc} is affected twice as strong as R_{mb} (Figure 7.2a), and in which R_{mb} is affected twice as strong as R_{mc} (Figure 7.2b). The *CRS* has a flatter line, which means that individuals will have to work harder for the same return compared to the unchanged situation, and because the environment became less good also the maximum *CRS* decreased. The maximum value for *FRS* decreased, because a bad environment lowers the expected future reproductive success so there is less to lose. Because maximum investment in current reproductive success is defined as the level of investment that reduces *FRS* to 0, the line is flatter than before. To put these predictions in the perspective of the results of **chapter four**, Figure 7.2c shows the predicted change for non-migratory individuals.

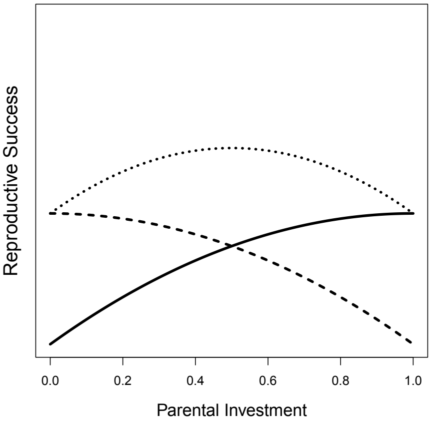


Figure 7.1. Current reproductive success (*CRS*, solid line), future reproductive success (*FRS*, dashed line) and lifetime reproductive (*LRS*, dotted line) as a function of parental investment. Optimal duration of investment I^* is 0.5.

The question thus is, how do increased predation danger and increased competition for food affect R_{mc} and R_{mb}? During spring migration, while refuelling at a stopover site, the parents have to store sufficient energy reserves to breed successfully during the next breeding attempt (*FRS*) (Drent and Daan 1980). The offspring (at that moment the *CRS* of the parent) ‘only’ need the amount of energy to travel to the breeding grounds. The effect of increased food competition will thus be more severe for the preparing parent (and thus *FRS*) than the offspring (*CRS*). The effect of predation danger, however, will be different. Predation danger will mainly affect the inexperienced young, because the adults have been more exposed to predators before and will therefore spot predators more easily (Caro 2005). Consequently the parents investment in *CRS* will return less because there is a larger chance that the parents lose this investment (flatter slope). With competition the offspring may be a bit leaner, but that affects the *CRS* less than the lethal effects of predation. Concluding, these theoretical predictions of both

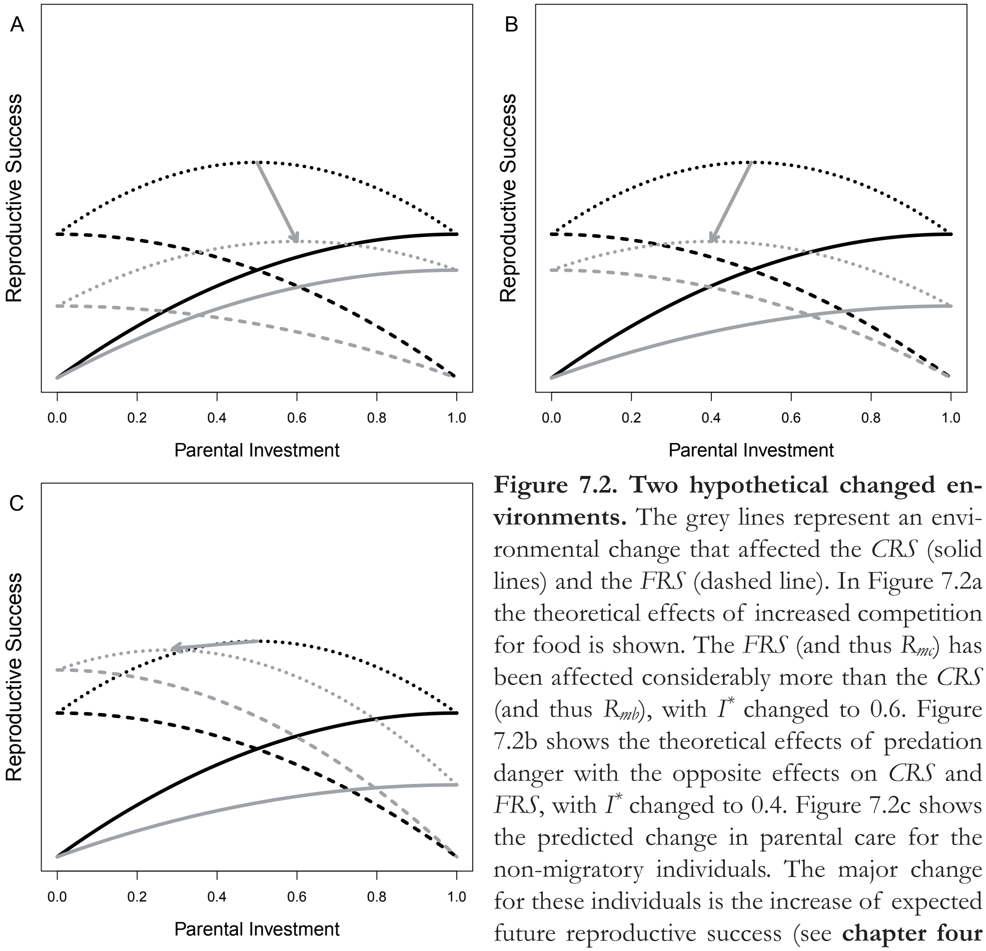


Figure 7.2. Two hypothetical changed environments. The grey lines represent an environmental change that affected the *CRS* (solid lines) and the *FRS* (dashed line). In Figure 7.2a the theoretical effects of increased competition for food is shown. The *FRS* (and thus R_{mc}) has been affected considerably more than the *CRS* (and thus R_{mb}), with I^* changed to 0.6. Figure 7.2b shows the theoretical effects of predation danger with the opposite effects on *CRS* and *FRS*, with I^* changed to 0.4. Figure 7.2c shows the predicted change in parental care for the non-migratory individuals. The major change for these individuals is the increase of expected future reproductive success (see **chapter four** for details), with I^* changed to 0.29.

competition and predation suggest increased predation danger to be a more likely cause of delay in commencement of spring migration.

This is an exciting framework to conduct field studies in, and the reasoning outlined here provides plenty of testable hypotheses. For example, field studies or experiments could test the hypothesis that *FRS* (the next breeding attempt) is more affected by food competition than the *CRS* (the already present offspring) in migrating barnacle geese or that the behaviour of young individuals is more affected by predation danger than the behaviour of adults.

This theoretical reasoning generated a number of hypotheses on the functional consequences of migratory change in barnacle geese. Hence, questions on other species, such as the Brent goose *Branta bernicla* for which no migratory changes are reported, arise. Why did brent geese not change their migratory behaviour? How is the *FRS* and *CRS* of brent geese affected by both food competition and predation danger, and can a functional approach explain why no changes have been observed?

2) Phylogenetic view on migratory change

When examining the phylogeny of the Anatidae (Gonzalez et al. 2009) and the parental care systems throughout this phylogeny (Kear 1970), it becomes clear that long parental care is the rule in geese and swans (Anserinae), whereas short parental care is the rule in Anatinae (ducks) (Figure 7.3). Within the Anatinae, the Tadornini (Shelducks and Sheldgeese) and Tachyeres (Steamer ducks) are exceptions with much longer forms of parental care. This phylogenetic pattern suggests that changing the type of parental care system is not likely, but the results in **chapter three** and four show that barnacle geese can rapidly adjust their duration of parental care to new situations. Alternatively, it could be that variation in parental care within these species is poorly recorded and that in many more species individuals adjust the level and duration of parental care continuously.

Mayr (1942) describes the culturally inherited migration, with its strong natal philopatry, as key explanation for the number of different races within geese. Also more recent studies suggest the importance of the strong natal philopatry for speciation in geese (Anderson et al. 1992; Fowler et al. 2004), as it increases the expected relatedness among individuals within colonies. Shortening parental care, changing migratory habits and the decreasing importance of migratory traditions within barnacle geese can potentially change this process of speciation in geese.

3 & 4) Mechanistic and ontogenetic view on migratory change

After approaching the migratory and parental care changes from a functional and phylogenetic perspective separately, I chose to combine the mechanistic and ontogenetic approach. In **chapter two** I have suggested a possible mechanism via which new migratory behaviour can emerge, and especially how this process can accelerate. The proposed mechanism is that with delayed migration, and advanced termination of parental care a gap between the end of the parent-offspring association and the commencement of spring migration has emerged. This gap reduces the chance that offspring associates with their parents at the moment that migratory decisions are being made and hence decrease the chance that the offspring copies the parents' strategy. Crucial in this reasoning are the assumptions that: 1) offspring has no innate migratory strategy and offspring can copy the migratory strategy from parents. Experiments with lesser white-fronted geese *Anser erythropus* (Von Essen 1991), canada geese *Branta canadensis* and trumpeter swans *Cygnus buccinator* (Sladen et al. 2002) showed that juvenile geese can learn a previously unknown migratory strategy from foster parents. 2) Without parents, offspring

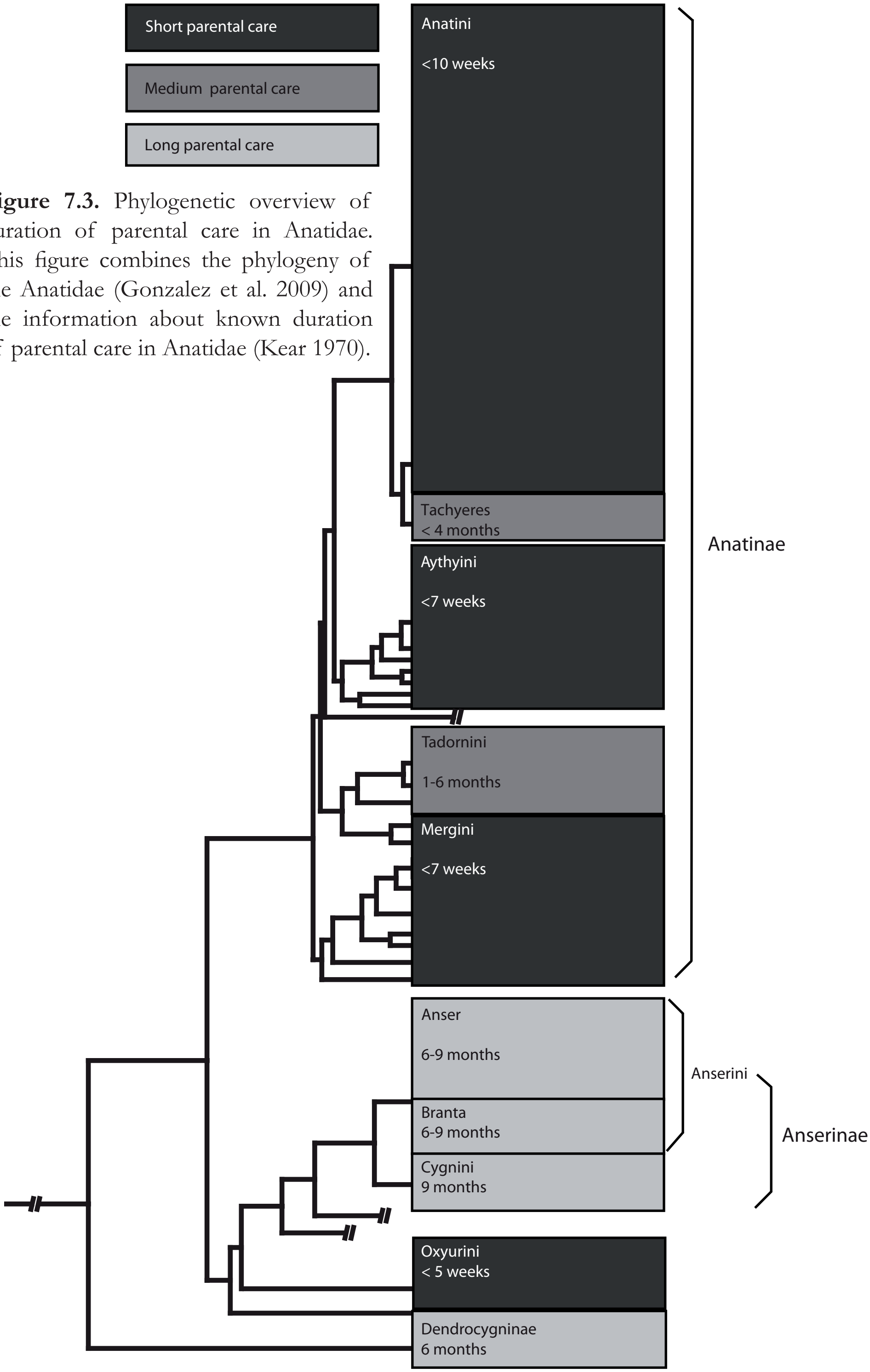


Figure 7.3. Phylogenetic overview of duration of parental care in Anatidae. This figure combines the phylogeny of the Anatidae (Gonzalez et al. 2009) and the information about known duration of parental care in Anatidae (Kear 1970).

(Adapted from Gonzalez *et al.* 2009 and Kear 1970) explore new locations (Baker 1978). 3) there is more than one potential successful migration strategy (e.g., multiple suitable breeding locations).

Here I show that the emergence of new migration strategies can be explained with a few simple mechanistic rules. To formalize this logic, and to show the consequences of these mechanistic rules, I present a model that shows the influence of culture, and timing of migration on migratory change. This model simulates individuals that acquire a migratory strategy during their first year, after which they are able to transmit it again to their offspring. In that sense it combines the mechanism of transmitting migration with the ontogenetic development of migratory behaviour of an individual.

Model description

The model is inspired by the logic of the model on dispersal proposed by Hamilton and May (1977). In their model individuals produce offspring with a certain tendency of dispersal to other sites. They show that the evolutionarily stable strategy from the parents point of view is to have at least some proportion v of offspring to disperse and explore potential other sites, even in stable habitats without extinction. In their model all exploratory offspring from all occupied sites end up in a pool of exploratory offspring. These offspring are then divided over all potential sites, taking into account that a proportion p of these migrants dies. At each site all residential offspring (offspring that was produced in that site and that was not-exploratory) and exploratory offspring compete for reproduction. Eventually, all adults who do not produce exploratory offspring are outcompeted (see also Comins et al. 1980 for more details).

In my case it is not sites that can be explored but migration strategies. These are characterized in our model by breeding sites. The further away the breeding site is from the wintering site, the longer the migration is. By using this simplification, we can approach the exploration of new migration strategies as a dispersal problem. Individuals disperse from some migration strategy to another and by doing so they prevent extinction when the original strategy fails, or when the habitat is invaded by competitors who happen to have more exploratory behaviour. This exploration comes with the cost of losing offspring to risky explorations, but the costs of not exploring potential new migration strategies are even higher: extinction.

In the model individuals migrate from a breeding area to a wintering area and back. Our landscape is a one-dimensional space i, with $i=0$ being the wintering location and $i=x$ being the breeding location with $0 \leq x \leq 1$ (step size: 0.1). Breeding can occur anywhere, and the success of breeding is equal for all breeding areas. Each generation consists of one year of 365 days. At $t=1$, the beginning of the year, an individual, from now on called 'parent', starts at the site where it ended ($T_{MAX}= 365$) the previous year, and is accompanied by offspring.

During the year the parent decides where to go, based on four time-dependent decision rules. In the first generation the start location always is i=1. First, before autumn starts at T_{autumn}, an individual should stay at the breeding site. Second, when autumn starts, an individual should migrate southward until arriving in the wintering site (i=0) with a migration speed of 0.025 $[x\ d^{-1}]$. When migrating from the most northern site to the wintering site this takes 40 days. Third, stay in the wintering site until spring starts at T_{spring}. Fourth, when spring starts, migrate with the same speed northwards to the breeding area. The moments set for autumn migration and spring migration are roughly in spring and autumn (T_{autumn}=95, T_{spring}=270 unless specified differently).

The decision rules for offspring are a bit more complex. Basically, the offspring stays with the parents, until the family splits up. This splitting up is defined by the parent-offspring association, ranging between 0 and 1. At t=1 the parent-offspring association PA is 1. At some moment the parent-offspring conflict starts, resulting in decreasing parent-offspring association following a negative sigmoidal function starting at one and going asymptotically to 0. The logic behind this is that at first the parent-offspring conflict is not really strong, but it gets stronger after some time, and some association strength will remain for a long period. Theoretically, this could result in offspring staying with the parents until T_{MAX}.

The association strength serves as a threshold for leaving the parents or not. When a randomly generated number exceeds the threshold, the offspring leaves the parents. This randomly generated number has a lower limit of 0, and an upper limit defined by the importance of cultural association vs. innate information when making migratory decisions, C (cultural threshold) with $0 \leq C \leq 1$. When the upper limit is 0, offspring will not be affected by the parent-offspring associa-

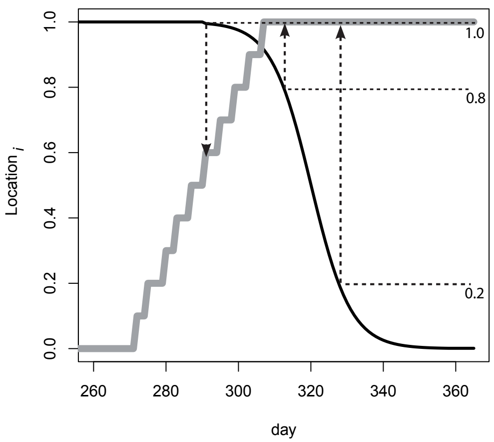


Figure 7.4 Schematic influence of culture threshold C. The grey line is the individual migrating from its wintering location (i=0) to its breeding location (i=1). The black line is the strength of the parent-offspring association (also ranging from 1 to 0). The dotted line with C = 1.0 shows that as soon as the parent-offspring association starts to weaken the chance that offspring leaves the parents arises, as indicated by the space between the parent-offspring line and the dotted line. With C = 0.8 and C = 0.2, this moment comes much later, when the parents and offspring already arrived at the breeding site of the parents. As the black line of the parent offspring association asymptotically goes to 0, an upper limit of 0 will never generate values larger than this association, and thus the offspring will always migrate to the parents breeding grounds.

tion and still migrate to the same location as the parents, as it would be when migratory behaviour was genetically inherited. With a upper limit of 1, offspring is most sensitive to reduced parent-offspring association: offspring leaves the parents sooner and starts exploration on its own. This variable thus influences the chance that the offspring starts deviating from the parents' strategy. In Figure 7.4 the effect of C is shown schematically.

However, leaving the parents comes with a cost of increased mortality for the offspring moffspring. This mortality is time and site dependent. This because some sites (all >0.4) are too harsh during winter. In the case that parents die before autumn migration, offspring will have a very tough time surviving four months of winter on their own. When offspring leaves the parents it has a probability $P_{explore}$ (0.25) of exploring new sites. If an individual explores during a time step it will move one site northward or southward with equal probability. When it does not explore, it will remain at its current site.

When offspring is still alive at T_{MAX}, it will store that site as its future destination. It has acquired, so to say, information during its first year on possible breeding locations. It will behave as a parent with new offspring from t=1 in the next year. If the parent survives until T_{MAX} it will reproduce as well, and behave similarly in the next year. In theory, parents have eternal life, but because they also have a mortality rate per day, they will die eventually with $P_{survival}$ (0.9998 d^{-1}). In the analyses I compare simulations as if they are different genotypes.

I do not take density dependence into account in this model. I mainly do so for modelling convenience, but also because it is not important for answering our questions. For a population perspective one could treat all parents as the informed part of a population, and the offspring as the uninformed part of a population. When for some reason, for example juvenile exploratory migration, the uninformed part of the population no longer associates with the informed part of a population, new information is potentially acquired, at the cost of increased mortality. The results of the genetic analysis in **chapter six** also suggest that density dependence did not play a crucial role in the expansion of the breeding range, and thus emergence of new migratory strategies.

Migratory delay

One of the central themes in this thesis is the delay of migration by Russian barnacle geese (**chapter two** and **chapter three**). With this simulation I show how such a sudden delay affects exploratory behaviour, and the variation in migratory strategies. I simulated delayed commencement of spring migration by comparing simulations with different dates for the commencement of spring migration and evaluated the effect of this on the following exploration measures. The first is the time in generations it takes for the

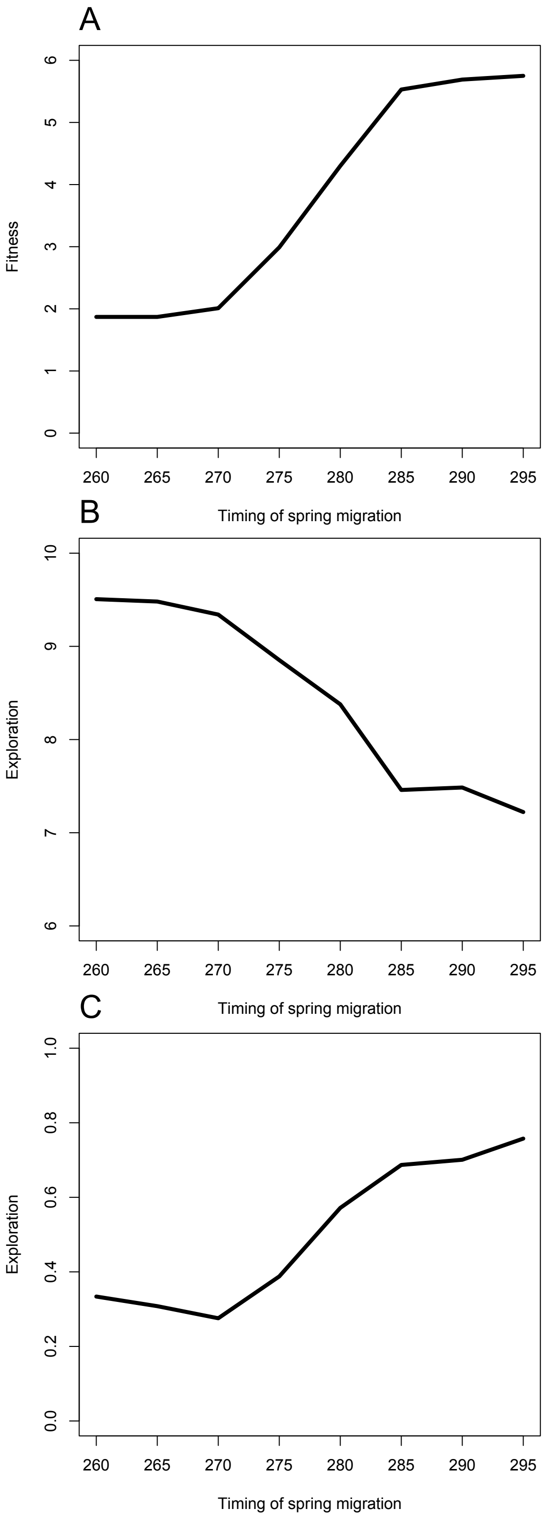


Figure 7.5. Migratory delay and consequences for colonization. A) Shows the fitness with delay in migration. B) Shows the exploration speed expressed by the generation in which location *i*=0 was colonized (low values= high speed). C) Shows the cost of delayed migration, by increased offspring mortality.

individuals to colonize the wintering site as a year round breeding site, and as such lose their migratory behaviour. The second is the total number of breeding sites occupied after 50 generations. Each simulation starts with an individual breeding at *i*=1.0. Because this represents the success of the genotype (an individual with the given set of parameters and rules), I hereafter refer to this measure as fitness. If only one strategy is occupied it means that there is no variation in migratory behaviour.

In addition to benefits of explorative behaviour there are costs, as advanced termination of parental care increases the offspring mortality. I express this mortality by evaluating when an explorative offspring is unsuccessful in its exploration (i.e., when it dies) divided over the number of generations a genotype survived. These simulations show that indeed a shift in migration affects exploration speed, and consequent colonization of new breeding locations (Figure 7.5). The number of breeding locations occupied after

10 generations increases from approximately three with spring migration date of 260 to approximately 6 with spring migration date of 290 (Figure 7.5a), and the exploration speed increases from needing 9.5 generations to colonize $i=0$ to approximately 7 (Figure 7.5b). Also the costs increase with this extra exploration, but judging from the fitness results these costs are lower than the benefits. When there is variation in timing of migration, this mechanism will give rise to individuals that are more likely to change migration direction or breeding location. In the case of barnacle geese there was already variation in timing of migration in the 1970s, as illustrated by Eichhorn et al (2008, Figure 4). The here presented mechanism may have accelerated the changes observed. Future studies of bird migration should thus not only focus on concepts like flyways (which is basically the route that most individuals follow), or mean departure or arrival dates, because it will probably be the odd individuals, such as individual Brent geese or Red-breasted geese Branta ruficollis found in flocks of barnacle geese, that can provide insight in potential changes.

Culture and parental care

In geese, culture plays a very important role for the transmission of migratory behaviour. This in contrast to other bird species, such as black caps where migration direction (Helbig 1991) and migratory tendency (Pulido and Berthold 2010), are genetically determined. Here I show how, with the above mentioned rules, culture and the duration of parental care affect explorative behaviour.

These simulations in which culture, C, was varied with the duration of parental care, show that the optimal duration of parental care decreases with decreasing C (Figure 7.6a, page 107). The simulations also show that the speed of exploration increases with shorter duration of parental care (Figure 7.6b, page 107) With longer parental care it takes more generations to colonize $i=0$ as breeding location, or this location is not colonized at all (after 50 generations). So, shorter parental care increases the exploratory behaviour, but it also decreased the offspring survival. Figure 7.6c (page 107) shows that with shorter parental care, the mortality of offspring increases. When these two opposing factors, exploration speed and offspring survival are multiplied, the result is strikingly similar to the calculated fitness, suggesting that individuals in this model optimize between survival of offspring and colonization of new breeding areas (compare Figure 7.6a and 7.6d, page 107).

These simulations also show the importance of how migration is transmitted and how important the parent-offspring interactions are in this process. When offspring has genetic information of migration ($C=0$) little exploration occurs, with more extinctions as a consequence. It has been shown that also genetically programmed migrants can reduce migratory activity within a few generations, but this has only been shown in lab studies (Pulido and Berthold 2010), and changes of direction have only been shown with crossing individuals from different populations (Helbig 1991). It would be very interesting to know what part of migratory behaviour is genetically and culturally transmitted in species that have trouble adjusting to changing environmental conditions. The lessons learned from the mechanisms of (barnacle) geese and their success of changing migratory behaviour may help identifying what the bottlenecks in adaptive capacity of other species are.

Concluding

Addressing these four questions provides insights into the functional, phylogenetic, mechanistic and ontogenetic aspects of migratory changes in barnacle geese and the role of parental care therein. I have shown that a functional approach can help us predict how different competing hypotheses on the delay of spring migration would affect the duration of parental care, and based on these predictions I suggest that predation danger is a more likely cause of this delay than competition for food.

Phylogenetically, it is clear that the shorter parental care in non-migratory barnacle geese is very novel. None of the other geese do this, and parental care duration seems a conservative trait within the Anatidae family. This suggests that either the non-migratory barnacle geese show unprecedented adaptation to a change in life style (from migratory to non-migratory), or that parental care systems within the Anatidae are poorly recorded and understood.

With the mechanistic model on the ontogeny of migratory behaviour I show the importance of culture on emergence of new migratory behaviour, and that a delay in spring migration can cause sudden increased explorative behaviour of juveniles and colonization of new breeding locations. It also shows that the duration of parental care is affected by the trade-off between offspring survival and exploring new opportunities for future survival. This mechanism will be especially important during times of rapid environmental changes, because it is in those times that novel behaviour is extra rewarded.

Finally, the first lines in the introduction of this thesis speak of anomalies in nature and that at first sight a non-migratory migrant seems anomalous. However, this thesis opposes this view and presents a logical evolutionary explanation for this non-migratory behaviour and shows how these non-migratory migrants have adapted to a new life style.

Colour figures Chapter 5

Figure 5.1. Phred quality scores per position.
Average phred scaled quality scores of two paired-end lanes of 101 bp. The dotted line indicates the cut-off point for further analysis and shows that the minimum average quality score on position 62 is 17 (error prob.: 1/50.12). The different colours indicate the different lanes. One paired-end lane is plotted in dark blue and light blue and the other in dark green and light green.

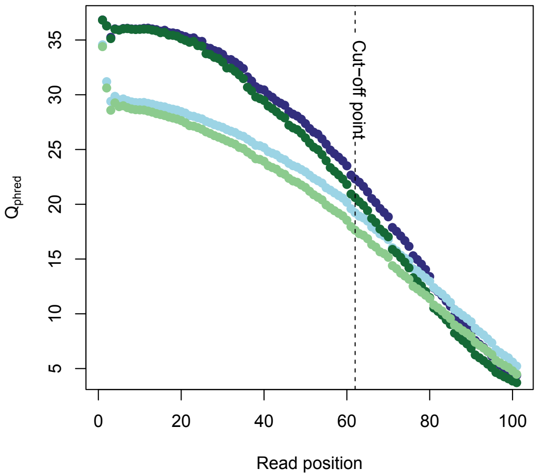


Figure 5.2. Detected and selected SNP per position.
The number of detected (blue) and selected (red) SNPs per read position (scale on the left y-axis). The open circles indicate the TS/TV ratio for the detected SNPs per position (scale on the right y-axis).

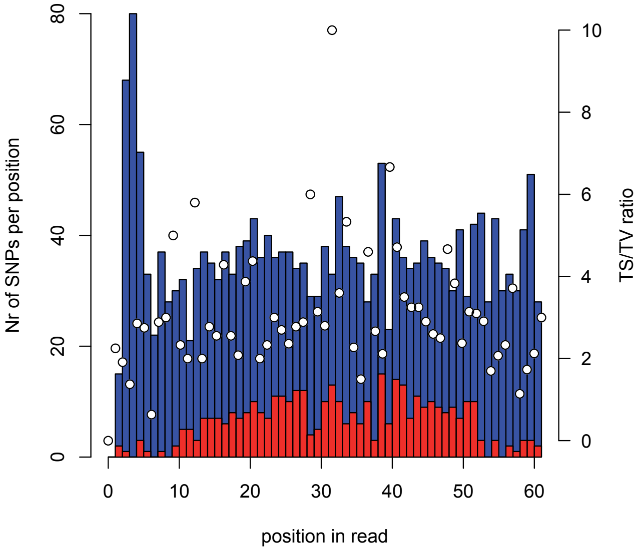
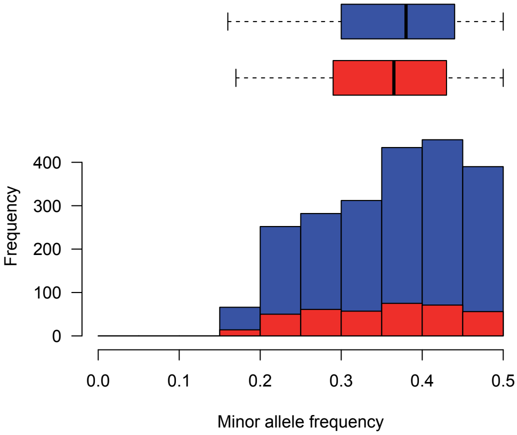


Figure 5.3. Minor allele frequencies.
Minor allele frequencies (MAF) of detected (blue) and selected (red) SNPs. Mean MAF of detected SNPs was 0.37, mean MAF of selected SNPs was 0.36. The inserted box plots show the median MAF of both the detected (blue) and the selected (red) SNPs.



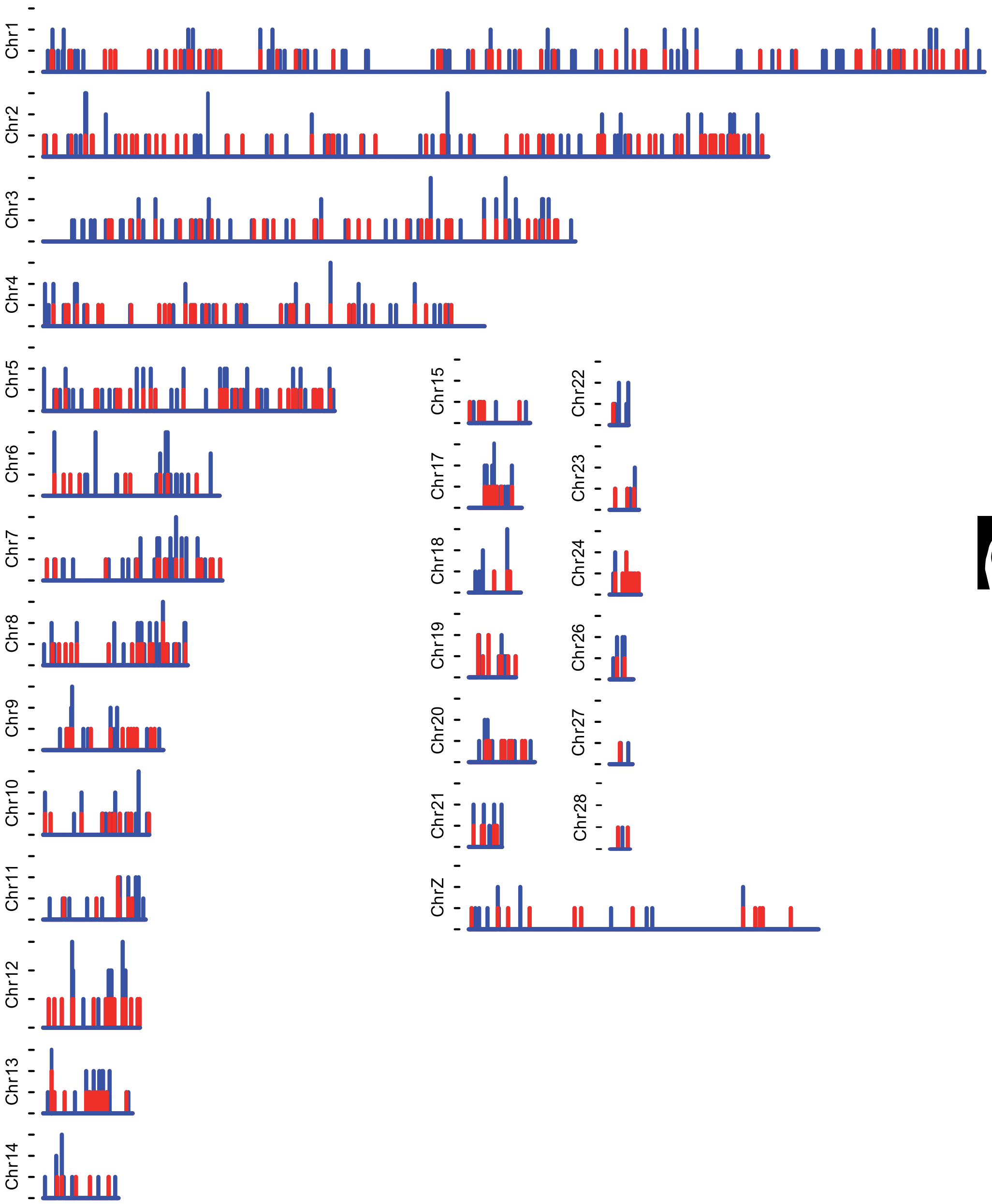


Figure 5.4. Map of detected and selected SNPs over the chicken genome.
Per chicken chromosome the number of detected SNPs (blue) and selected SNPs (red) per 200kb bin is shown. Because the bin size is 200 kb and the minimum distance between selected SNPs is less than 200kb for the smaller chromosomes two SNPs per bin occurred in chr 8, chr 11, chr 13, chr 19 and chr24.

Colour figures Chapter 6

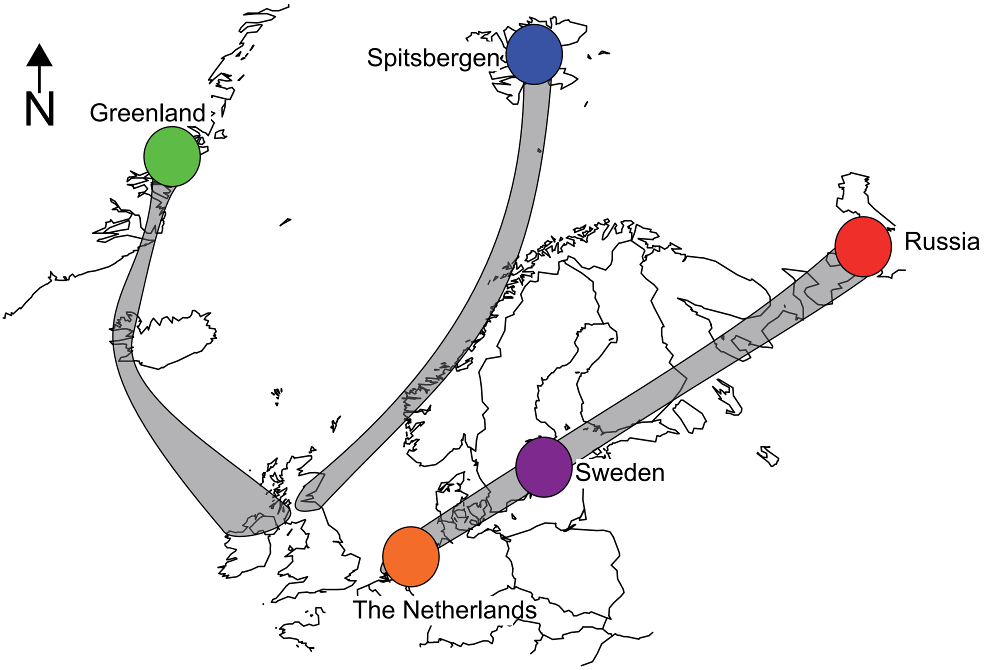


Figure 6.1. Map of Barnacle Goose populations.
Colours correspond with the colours in the other figures. The separate migratory flyways are indicated in grey.

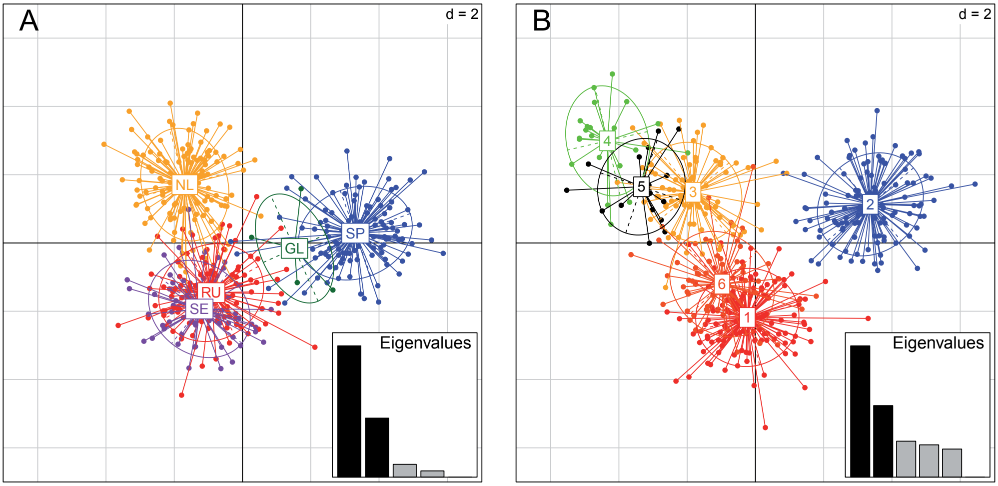


Figure 6.2. Scatter plot of prior and posterior clusters.
In the left panel (A) the individuals are plotted with a priori defined populations (GL: Greenland, SP: Spitsbergen, RU: Russia, SE: Sweden, NL: The Netherlands). In the right panel (B) the individuals are assigned to populations a posteriori, i.e., after determining the number of clusters by the program, instead of forcing into known populations. Cluster 2 corresponds largely with Spitsbergen and cluster 1 corresponds to Russia and Sweden together. In cluster 6 individuals

from all populations are present, but mainly from the Netherlands, clusters 3, 4 and 5 almost completely consist of individuals from the Netherlands. The colours in Figure 2a correspond with the colours in Figure 3a and the colours of Figure 2b correspond with the colours of Figure 3b. The bar graph insets indicate the amount of variance explained by the two discriminant eigenvalues used for plotting. Both plots have the same scale on both axes, as indicated by the d=2 in both graphs. Ellipses are inertia ellipses calculated by the variance of both pc-axes and represent 67% of the variance.

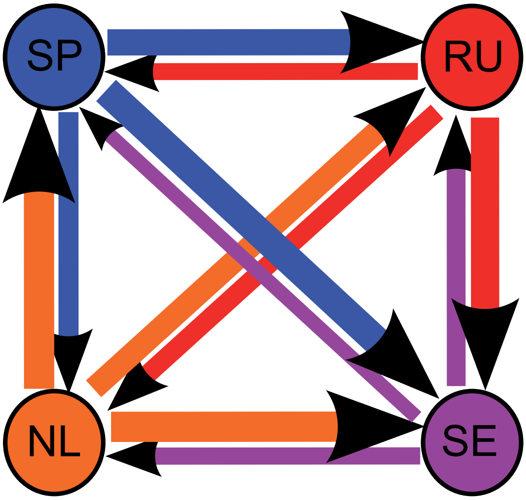


Figure 6.4a. Schematic overview of migration rates.
The migration rates between all populations are schematically shown by the width of the lines and the arrow heads. Colours represent population of emigration.

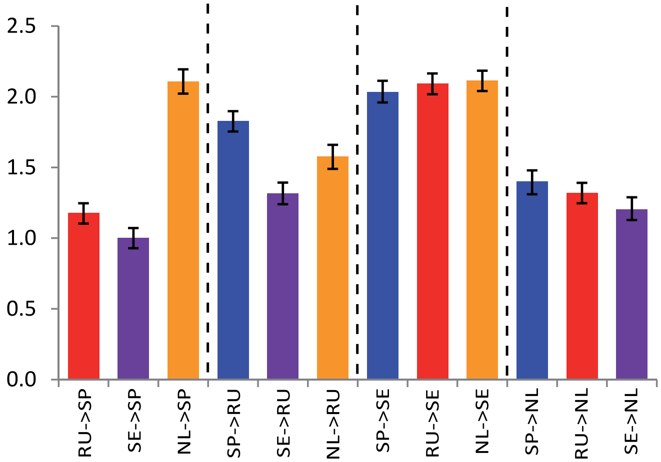
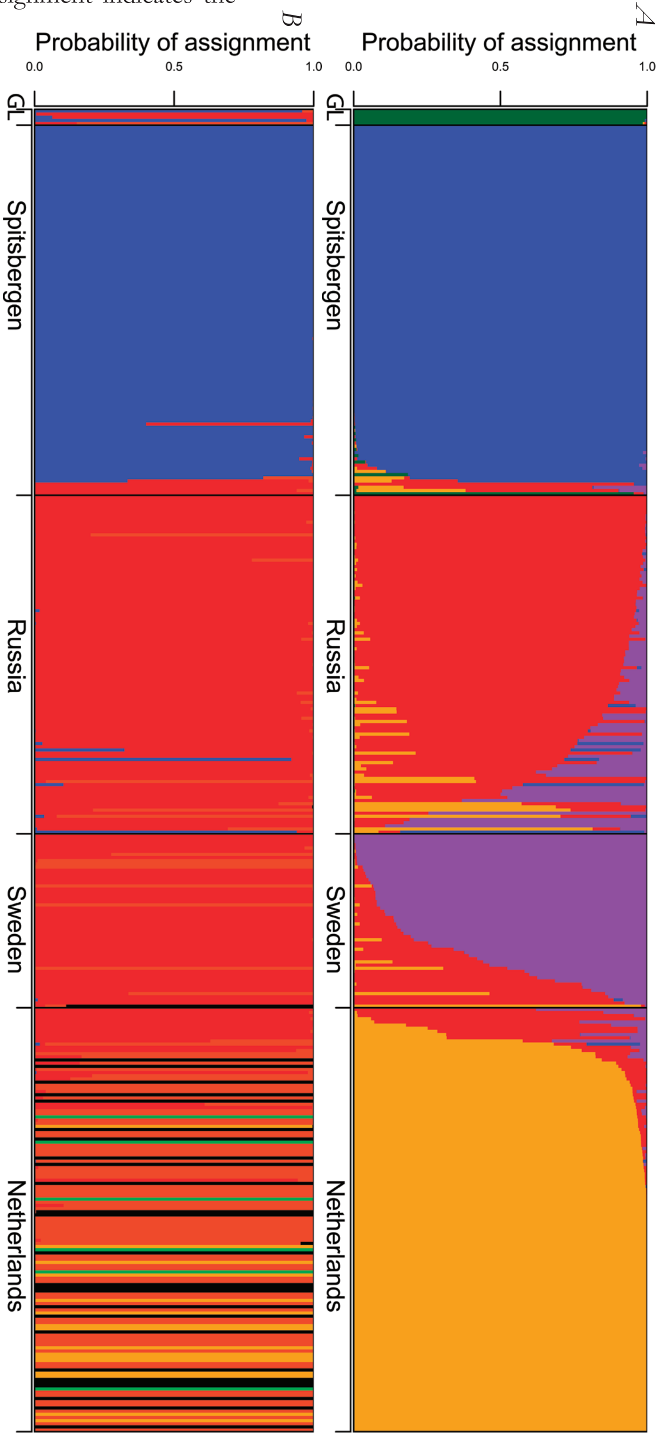


Figure 6.4b. Migration rates with confidence intervals.
The modes of the scaled migration rates with confidence 95% confidence intervals are shown. Colours represent the population of emigration. Dashed lines separate the immigrated populations.

Figure 6.3. Stacked bar graph of assignment probabilities per individual. In the upper panel (Figure 6.3a) populations of the individuals were defined a priori. The probability of assignment indicates the probability that each individual was assigned to its a priori set population. In the lower panel (Figure 6.3b) no populations were defined a priori. Instead individuals were assigned to one of the clusters that were detected by the software. Both Figure 6.3a and 6.3b consist of 418 stacked bars, in which each bar is one individual and the order of the individuals is the same in both graphs. If an individuals was assigned to multiple clusters, bars were stacked. In Figure 6.3a it is clear that there are individuals that are assigned to the population in which they were sampled (for example all the blue in the Spitsbergen part, all the red in the Russian part, the orange in the Dutch part). However some individuals sampled in one population were assigned with a larger probability to another population, as a result of recent immigration into that population. Figure 6.3b shows that from the detected clusters (shown in Figure 6.2b), clusters 3, 4 and 5 almost completely consist of Dutch individuals, and that cluster 1 includes the Russian and Swedish population and a small part of the Dutch population. Cluster 2 clearly represents the Spitsbergen population. The colours in Figure 6.2a correspond with the colours in Figure 6.3a and the colours of Figure 6.2b correspond with the colours of Figure 6.3b.



Colour figures Chapter 7

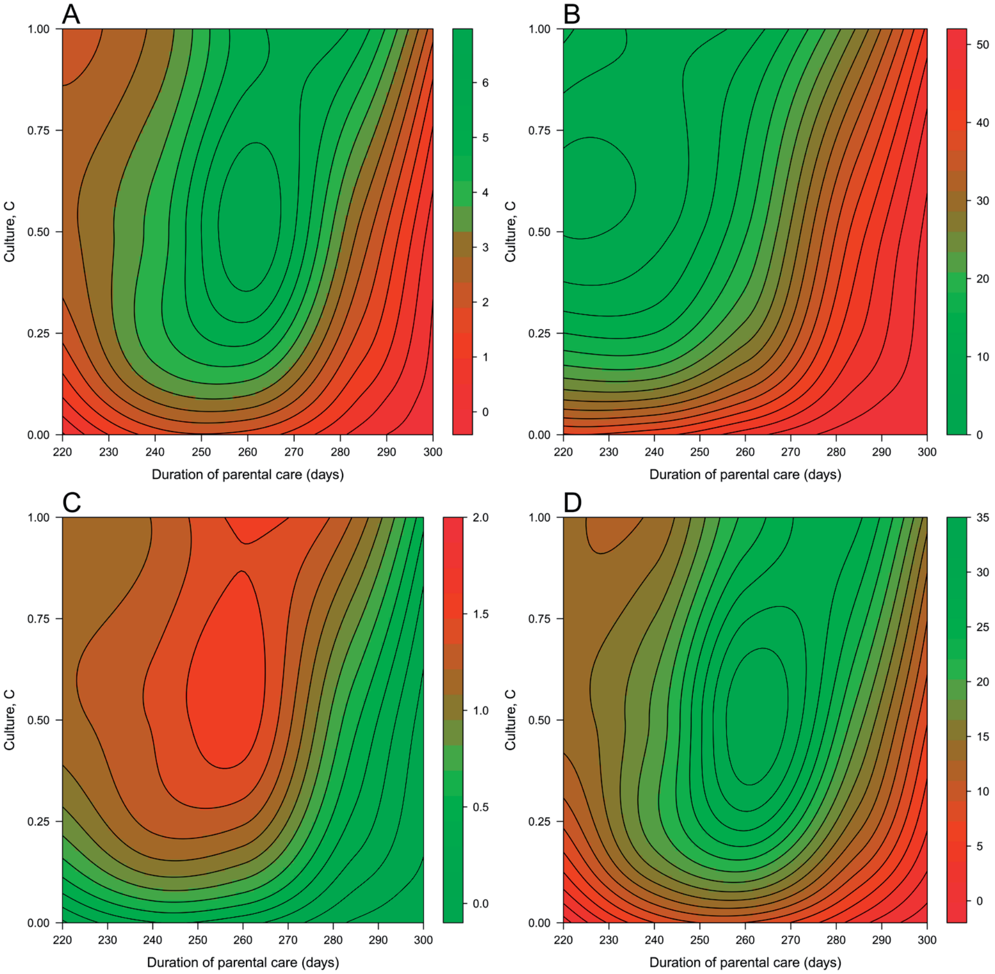


Figure 7.6. Influence of culture on the optimal duration of parental care. A) Shows the fitness (number of strategies occupied at generation=50). For each level of C, there is an optimal duration of parental care, and this optimal duration of care decreases with decreasing culture. B) Shows the exploration speed, presented as the generation in which i=0 was colonized as breeding location. A lower number of generations needed means faster exploration. C) Shows the costs of shorter parental care, expressed by offspring mortality after exploration. D) Shows the result of multiplying the costs and the speed of exploration.

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Summary

In the migratory behaviour of the Barnacle Goose *Branta leucopsis* several changes have occurred over the past few decades. Barnacle geese breeding in Russia have delayed the commencement of spring migration with approximately one month since the 1980s, new populations have emerged in former stopover areas in the Baltic Sea region, and a non-migratory population has emerged in the wintering area in The Netherlands. This thesis aims to understand these changes.

First, I studied the delay in commencement of spring migration. In the 1970s and 1980s, barnacle geese commenced spring migration half April, whereas spring migration now commences half May. I used a dynamic programming model to test three different possible explanations of delay in migration: 1) Climate change, because geese follow a green wave of fresh plant growth during spring migration, and are thus expected to be sensitive to increasing spring temperatures. 2) Competition for food during stopover because the population migrating to Russia has rapidly increased during the period in which the migration change occurred. 3) Predation danger during stopover because the number of avian predators such as White-tailed Eagles has drastically increased in the Baltic stopover area. The model showed that a delay of one month is adaptive in both the case of competition and predation danger. Strikingly, predation danger has received very little attention so far in goose studies.

Migration strategy in geese is not genetically but culturally inherited, especially from parents to offspring via an extended period of parental care. Because this thesis focused on understanding migratory change, I focused on the parental care behaviour and the parent-offspring association because a change in migration was expected to be preceded by a change in the parent-offspring association. Because spring migration had delayed, the question arose whether the termination of parental care also had delayed. This would indicate a mechanistic link between the decision of commencement of migration and the termination of care, and would allow the barnacle geese to continue transmission of the migratory strategy to their offspring. Therefore, I quantified parental care throughout the season from autumn migration in Estonia to wintering in the Netherlands and through spring migration in Estonia. To quantify parental care, I compared parental geese (geese with offspring) and non-parental geese (geese without offspring). I showed that termination of parental care had not delayed but advanced as compared to the earlier situation, leaving a gap of two months between the estimated end of parental care (March) and the commencement of migration (May). This longer period of ‘adolescence’ and the accompanying exploratory behaviour may have strong influence on the amount of new colonization attempts by these abandoned offspring.

In addition to delayed commencement of spring migration, also a non-migratory population emerged in the Netherlands. Life-history theory predicts that 1) higher expected future reproductive success leads to shorter parental care and 2) decreased benefits of parental care lead to shorter parental care. Both situations apply to the non-migratory population as compared to the migratory population of barnacle geese. Migration is a dangerous life-style, and has become even more dangerous as I showed earlier. Additionally, the non-migratory offspring encounters few dangers, making the benefits of parental care for the parents smaller. Hence, I compared the duration of parental care between migratory and non-migratory barnacle geese. To this end, I also quantified the parental care of the non-migratory population from autumn until spring. I showed that non-migratory barnacle geese take care of their offspring 21% shorter than migratory barnacle geese and terminate care already in November. This suggests a rapid adaptive adjustment of parental care coincident with altered migration.

To understand the colonization history of the different populations of the Barnacle Goose, I developed a set of 384 Single Nucleotide Polymorphisms (SNP) specifically for the Barnacle Goose. By genotyping 418 individuals from Greenland, Spitsbergen, Russia, Sweden and the Netherlands (all major populations) I identified significant population structure. The results show that after previously having been separated, population admixture occurs now between all populations, indicated by significant linkage disequilibrium. Because the traditions of migratory behaviour promote differentiation between populations, this admixture suggested that these traditions had broken or had become weaker. We also show that the colonization of the Netherlands is not likely to have occurred by the Swedish population (which emerged ten years before the Dutch population emerged). The Russian and Dutch population are much more alike than the Swedish and Dutch population, indicating colonization of the Netherlands by formerly Russian barnacle geese.

In the synthesis I showed that we can use life history trade-offs as indicators of environmental change. Based on the shortening of parental care I concluded that predation danger is a more likely explanation for the commencement of spring migration than food competition in the Baltic. I also showed that the shortening of parental care in the Barnacle Goose is not the norm in the Anatidae family, where the form of parental care is assumed to be very conservative. The observed change in our study showed that either the non-migratory barnacle geese adjusted their parental care unprecedentedly, or that the parental care systems in this family are poorly recorded or understood.

Finally, I showed with a mechanistic model of cultural transmission of migratory behaviour that a delay in commencement of spring migration can explain sudden exploratory behaviour and colonization of new breeding areas at the cost of increased offspring mortality. The model also showed that the importance of culture on the transmission of migratory behaviour strongly affected the rate of exploration of new migratory strategies.

Samenvatting

Het migratiegedrag van de brandgans is de laatste tientallen jaren erg veranderd. De brandganzen die in Rusland broeden hebben het moment van vertrek vanuit Nederland in het voorjaar met ongeveer een maand vertraagd sinds de jaren 1980. Er zijn nieuwe populaties gesticht op plekken rond de Oostzee, die voorheen alleen als pleisterplaats tijdens de trek werden gebruikt. Tenslotte is er een niet-migrerende populatie ontstaan, die het hele jaar in Nederland blijven, wat voorheen alleen als overwinteringsgebied gebruikt werd. Dit proefschrift heeft ten doel deze veranderingen te begrijpen.

Allereerst heb ik het verlate begin van de voorjaarsmigratie bestudeerd. In de jaren 1970 en 1980 vertrokken brandganzen vanuit Nederland omstreeks half april. Nu daarentegen vertrekken ze pas halverwege mei. Ik heb een model gebruikt om drie verschillende mogelijke verklaringen hiervoor te onderzoeken: 1) klimaatverandering: ganzen volgen tijdens de migratie de zogenaamde groene golf van verse plantengroei en en met stijgende temperaturen in het voorjaar is het te verwachten dat de grasgroei verandert en dat dus ook de ganzen daar tijdens de trek op reageren. 2) concurrentie om voedsel op de pleisterplaatsen tijdens de voorjaarsmigratie: omdat de populatie brandganzen die naar Rusland trekt zeer snel is toegenomen in de periode waarin ook de vertraging is opgetreden. 3) gevaar van predatie tijdens de trek: het aantal roofvogels, zoals de zeearend, is drastisch toegenomen in de periode waarin de vertraging is opgetreden. Het model liet zien dat een vertraging van een maand adaptief was zowel in het geval van toenemende concurrentie om voedsel als in het geval van toenemend gevaar van predatie. Opvallend genoeg echter, is er erg weinig aandacht voor predatiegevaar geweest in het ganzenonderzoek tot nu toe.

Migratiegedrag wordt bij ganzen niet genetisch overgedragen, maar cultureel, en dan met name van ouders op jongen door middel van een zeer lange periode van ouderzorg. Omdat dit proefschrift ten doel heeft om verandering van migratiegedrag te begrijpen, heb ik specifiek naar het ouderzorggedrag en de ouder-jong relatie gekeken; Ik nam aan dat er voor een verandering in migratiegedrag eerst een verandering in de ouder-jong relatie nodig was. Omdat de voorjaarsmigratie vertraagd was, rees de vraag of ook het moment van stoppen van ouderzorg vertraagd was. Dit zou betekenen dat er een mechanistisch verband zou zijn tussen de beslissing wanneer te beginnen met de voorjaarsmigratie en de beslissing wanneer te stoppen met zorgen voor de jongen. Zo'n verband zou betekenen dat brandganzen het moment van stoppen met zorg aanpassen aan het moment van migratie om zo de jongen in staat te stellen het migratiegedrag over te nemen. Daarom heb ik de ouderzorg gekwantificeerd van de herfstmigratie in Estland en het overwinteren in Nederland tot en met de voorjaarsmigratie in Estland. Om de ouderzorg te kwantificeren heb ik ganzen met jongen (ouders) vergeleken met ganzen zonder jongen (niet-ouders). Het bleek dat het stoppen van de ouderzorg niet later plaatsvond maar juist eerder, vergeleken met eerdere studies, en dat daardoor een gat van twee maanden tussen het einde van de zorg (maart) en het begin van de voorjaarsmigratie (mei) ontstaan was. Deze lange periode van adolescentie en het bijbehorende verkennende gedrag, zou een grote invloed kunnen hebben op het aantal kolonisatiepogingen door deze in de steek gelaten jongen.

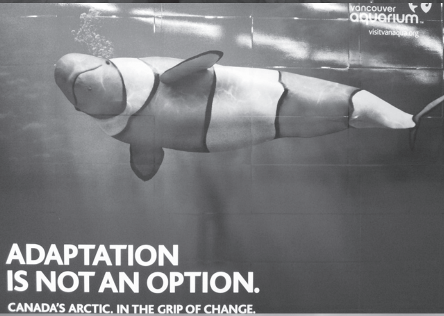
Naast de vertraging van de start van de voorjaarsmigratie, is er ook een niet-migrerende populatie ontstaan in Nederland. Levensgeschiedenistheorie stelt dat 1) hogere verwachtingen van toekomstig voortplantingssucces leiden tot kortere ouderzorg en 2) verminderde voordelen van ouderzorg leiden tot kortere ouderzorg. Beide situaties zijn van toepassing op deze nieuwe niet-migrerende populatie in vergelijking met de migrerende populaties brandganzen. Migratie is een gevaarlijke onderneming, en is zoals eerder vermeld nog gevaarlijker geworden. Daarbij komen de niet-migrerende jongen weinig gevaar tegen, wat de voordelen van ouderzorg voor de ouders vermindert. Om deze voorspellingen te toetsen heb ik de tijdsduur van ouderzorg van migrerende en niet-migrerende brandganzen vergeleken. Hiervoor heb ik de ouderzorg van de niet-migrerende populatie, naast de al eerder genoemde migrerende populatie, gekwantificeerd. Het bleek dat niet-migrerende brandganzen ongeveer 21% korter voor hun jongen zorgen dan de migrerende brandganzen en deze ouderzorg al in november stoppen. Dit wijst op een snelle adaptieve aanpassing van de ouderzorg gepaard met een verandering in migratiegedrag.

Om de kolonizatiegeschiedenis van de verschillende populaties van de brandgans te begrijpen, heb ik een genetische markerset van 384 *Single Nucleotide Polymorphisms* (SNP) voor de brandgans ontwikkeld. Door 418 individuen afkomstig van Groenland, Spitsbergen, Rusland, Zweden en Nederland (de belangrijkste populaties) te genotyperen, kon ik een significante populatiestructuur identificeren. Ook bleek dat deze populaties, na eerder relatief gescheiden te zijn geweest, recentelijk meer uitwisseling hebben gehad, wat tot significante *linkage disequilibrium* heeft geleid. De tradities (door de culturele overdracht) van migratiegedrag verhogen differentiatie tussen populaties, en deze nieuwe uitwisseling duidt er dus op dat deze tradities gebroken of zwakker zijn (geworden). De resultaten laten ook zien dat het niet waarschijnlijk is dat de kolonisatie van Nederland als broedgebied niet via Zweden (welke populatie ruim 10 jaar eerder gesticht werd) plaatsvond. De Russische en Nederlandse populatie zijn meer gelijk aan elkaar dan de Nederlandse en de Zweedse, wat erop duidt dat kolonisatie van Nederland als broedgebied waarschijnlijk is gebeurd door brandganzen die voorheen in Rusland broedden.

In de synthese laat ik zien dat we levensgeschiedenisafwegingen kunnen gebruiken als indicatoren van milieuverandering. Ik concludeerde op basis van de kortere ouderzorg (bij de migrerende ganzen) dat predatiegevaar een logischere verklaring gaf voor het vertragen van de voorjaarstrek dan concurrentie om voedsel in het Oostzeegebied. Ik liet ook zien dat de verkorting van ouderzorg bij de niet-migrerende brandganzen niet gebruikelijk is in de familie van de Anatidae (eenden, ganzen & zwanen). Er wordt aangenomen dat het type ouderzorg (kort of lang) binnen deze familie zeer conservatief is. De waargenomen verandering in dit proefschrift duidt erop dat ofwel de niet-migrerende brandganzen hun ouderzorg hebben aangepast op een niet eerder vertoonde manier, ofwel dat de ouderzorg binnen deze familie weinig onderzocht of begrepen is.

Tenslotte laat ik met een mechanistisch model van culturele overdracht van migratiegedrag zien dat een vertraging van voorjaarsmigratie een plotselinge toename van exploratief gedrag kan verklaren en daarmee kolonisatie van nieuwe broedgebieden, ook als dit initïeel hoge sterfte onder de exploratieve jongen als gevolg heeft. Het model laat ook zien dat het belang van cultuur in de overdracht van migratiegedrag in sterke mate invloed heeft op de snelheid waarmee nieuwe migratiestrategieën ontdekt worden.


FURUNO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Being a Ph.D. candidate is quite well comparable to migrating to some distant location in order to lay some eggs. You have to make the right decisions, you have to learn the difference between good and bad ideas, you have to detect when you are on the wrong track, you have to be able to convince the people around you that you can continue in some direction, even while they think you’re a complete nutcase. But just like during migration, social interactions were crucial during the time working on my Ph.D. thesis. Whether they were reviewers and editors giving me a hard time, or colleagues coming up with brilliant ideas or crazy stories, or friends and family who make you forget about all the troubles of the thesis and made me enjoy life a bit more and fuel up some energy to move on again. Here, I would like to take the opportunity to thank you all.

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Dankjewel.

Biography

Matthijs Rudolf (Rudy) Jonker was born on March 13, 1982 in Nairobi, Kenya. He attended secondary school at the 'Emmauscollege' in Rotterdam, from which he graduated in 2000. He became a member of the 'Nederlandse Jeugdbond voor Natuurstudie' (NJN) in 1996, which sparked his interest in nature and in dragonflies in particular. Consequently, he enrolled in the B.Sc. Biology at Wageningen University in 2000, and specialized in ecology. Rudy kept himself busy with many extracurricular activities. During the academic year 2003-2004 he was a full-time member of the student council as a representative of the United Students (VeSte). From 2003-2005 he was a member of the Euroleague for Life Sciences Student Association, representing students from five European universities. During his entire study time he was an active member of student association SSR-W in Wageningen.

For his first M.Sc. thesis at the Resource Ecology Group, Rudy went to the Large Animal Research Station in Fairbanks, Alaska, USA to study foraging behaviour of Caribou. Rudy did his second M.Sc. thesis at the Netherlands Institute of Ecology in Nieuwersluis, studying migratory decisions of barnacle geese. In June 2007 he received his M.Sc. degree with honours. Already in March 2007, however, he started the Ph.D. research that led to this thesis at the Resource Ecology Group at Wageningen University. During his Ph.D. Rudy participated in several discussion groups, of which the Wageningen Evolution and Ecology Seminars (WEES) was most exciting. He was member of the organizing committee of the 15th European Meeting of PhD students in Evolutionary Biology (EMPSEB2009) together with colleagues from Groningen and Wageningen, where he was responsible for funding. Rudy attended several conferences, of which the ISBE 2010 in Perth, Australia was most notable. During his Ph.D. Rudy has developed into an evolutionary ecologist with strong interest in migratory behaviour and life-history evolution.

Publications

1) R.H.J.M. Kurvers, K. Van Oers, B. Nolet, **R.M. Jonker**, S. E. van Wieren, H.H.T. Prins and R.C. Ydenberg. **2010**. Personality predicts the use of social information.
Ecology Letters 13:829-837.

2) **R.M. Jonker**, G. Eichhorn, F. Van Langevelde, S. Bauer. **2010**. Predation danger can explain changes in timing of migration: the case of the Barnacle goose.
PLoS One 5(6) : e11369.

3) **R.M. Jonker**, M.W. Kuiper, L. Snijders, S.E. Van Wieren, R.C. Ydenberg, H.H.T. Prins. **2011**. Divergence in timing of parental care and migration in Barnacle geese.
Behavioral Ecology 22(2): 326-331

4) **R.M. Jonker**, R.H.J.M. Kurvers, A. van de Bilt, M. Faber, S.E. Van Wieren, H.H.T. Prins, R.C Ydenberg. Rapid adaptive adjustment of parental care coincident with altered migratory behaviour. *Evolutionary Ecology in press*

5) **R.M. Jonker**, Q. Zhang, P. Van Hooft, M.J.J.E. Loonen, H.P. Van der Jeugd, R.P.M.A. Crooijmans, M.A.M. Groenen, H.H.T Prins, R.H.S. Kraus. The development of a genome wide SNP set for the Barnacle goose Branta leucopsis. *Submitted*

PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

Review of literature (6 ECTS)
- Literature & data research

Writing of project proposal (4.5 ECTS)
- Ph.D. Project proposal Rudy Jonker

Post-graduate courses (8.5 ECTS)
- Migration ecology course; University of Lund (2007)
- Consumer resource interactions (2010)
- Advanced statistics (2008)
- Evolutionary dynamics (2010)

Laboratory training and working visits (4.5 ECTS)
- Work visit; Centre for Wildlife Ecology, Simon Fraser University (2009)

Deficiency, refresh, brush-up courses (3 ECTS)
- Laboratory Animal Science (2007)
- Ecology of life-histories (2009)

Competence strengthening / skills courses (3 ECTS)
- Scientific writing; WGS
- PhD Competence assessment; WGS
- Designing scientific artwork; WGS
- Mobilising your scientific network; WGS

PE&RC Annual meetings, seminars and the PE&RC weekend (1.5 ECTS)
- PE&RC Weekend (2007)
- PE&RC Day – Expect the unexpected (2008)
- PE&RC Day – On the origin of communication (2009)

Discussion groups / local seminars / other scientific meetings (7.5 ECTS)
- Bird migration group; PhD students form RUG, NIOZ, NIOO & WUR (2007)
- Forest & Conservation Ecology (2007-2009)
- Maths & stats group, participant and organizer (2008-2010)
- Wageningen Ecology & Evolution Seminars; organization & participant (2009-2011)
- NERN Meeting; poster presentation (2008)
- Netherlands Annual Ecology Meeting; oral presentation (2010)

International symposia, workshops and conferences (14.7 ECTS)
- Migration Ecology Course; University of Lund; presented proposal (2007)
- 14th European Meeting of PhD Students in Evolutionary Biology (EMPSEB); Einsiedeln, Switzerland; oral presentation (2008)
- 15th European Meeting of PhD Students in Evolutionary Biology (EMPSEB); Schoorl, the Netherlands; organizing committee (2009)
- Evolution of Society; The Royal Society, London, UK; attendant (2009)
- Workshop Resource Ecology Group Wageningen University & Centre for Wildlife Ecology Simon Fraser University; Vancouver, Canada (2009)
- Culture Evolves; The Royal Society, London, UK; attendant (2010)
- ISBE 2010; Perth, Australia; oral presentation (2010)
- Nederlandse vereniging voor Gedragsbiologie; attendant (2010)

Lecturing / supervision of practical 's / tutorials; 15 days (4.5 ECTS)
- Ecological Methods I (2008, 2009 and 2010)

Supervision of 4 MSc students
- Quantifying parental investment of migratory and non-migratory Barnacle geese
- Quantifying parental investment of migratory and non-migratory Barnacle geese (duo with the first)
- Shifts in migratory behaviour couse changes in parental care in the Barnacle goose
- Behavioural features of a migratory Barnacle goose population (student was awarded REG Thesis award 2009)