

Modelling the flyway of arctic breeding shorebirds

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Parameter estimation and sensitivity analysis

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ABSTRACT

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This report describes the derivation of parameter estimates for the model DYNAMIG for an arctic breeding shorebird, the Knot. DYNAMIG predicts the optimal spring migration of birds, like shorebirds and geese, that depend of a chain of discrete sites, to travel between their breeding grounds and their wintering grounds. An important parameter is the terminal reward, which describes the fitness consequences of arriving with a particular body condition at a particular time on the breeding grounds. We derived the terminal reward from field studies in Siberia carried out as part of this project. Other parameter values, like flight costs, maintenance metabolism and predation risk were derived from the literature. Predictions on aspects of the migration schedule with the parameterized model were partly correct and partly wrong. Suggestions are made how to remedy the discrepancies. An interesting prediction of the model that requires testing is that Knots breeding in Canada migrate via Iceland, whereas Knots breeding on Greenland migrate via Norway. A sensitivity analysis indicated that this prediction was quite robust.

Keywords: migration, dynamic programming, flyway model, terminal reward, flight cost, predation risk, energy expenditure, shorebirds, Knot, *Calidris canutus canutus*, *Calidris canutus islandica*

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Preface

This report was born in 1997 when two of the authors (BE and MK) organised a meeting in Wageningen to discuss plans to submit a project proposal to Stichting Toegepaste Wetenschappen STW to obtain funds to further develop dynamic migration models. Although the proposal, submitted to STW in 1998, achieved high grades it was not funded. However, subsequently MK obtained funds from the EU (FRAGILE project) to continue the work along the lines envisaged in the original project proposal, whereas BE obtained funds from the ministry of LNV (Noord-Zuid programma - project flyway modellering). We did not obtain double money to do a single job, because MK obtained funds to apply and develop the models for geese, whereas BE obtained money to apply and develop the models for shorebirds. Both projects benefited greatly from the cooperation. The modelling efforts of the postdoc in the FRAGILE project (SB), gave HS and IT the opportunity to devote much effort on expeditions to the arctic to study the relationship between arrival conditions and reproductive success in shorebirds. During the final year of the study, the NIOO provided occasional working space to BE to finish writing the report. Popko Wiersma was so kind to provide us with the original meteorological data on which he based his estimates of maintenance metabolic rates of Knots. Hans Meltotte provided us with weather data from Greenland. Will Cresswell, Alasdair Houston, John McNamara and Ron Ydenberg commented on proposals to change the way predation risk was modelled. Jan van de Kam was so kind to provide us with a photograph of Knots landing on the tundra still partly covered in snow.

Summary

Shorebirds are prominent long-distance migrants that depend on a chain of wetlands for their survival. Wetlands are a threatened habitat and many countries, including the Netherlands, have signed international agreements to protect these wetlands, e.g. the Ramsar Convention, European Birds Directive, European Habitats Directive, Natura 2000, The Convention on Biological Diversity, European Community Diversity Strategy, Bonn Convention and the African Eurasian Waterbird Agreement. Effective protection requires a tool to assess the consequences of habitat loss and habitat change along the migration route.

For an Arctic breeding migrant, the timing of activities (e.g. migration, breeding, moult) poses a particular challenge since these should be synchronized with appropriate conditions in their highly seasonal environments. This notably applies for the spring migration to the breeding grounds, which has been identified as one of the most sensitive parts of the annual cycle. Time of and state at arrival on the breeding grounds are likely correlates of a migrants' fitness since the time available for reproduction is restricted. However, when and in which state birds arrive on the breeding grounds highly depends on conditions encountered during migratory flights and more importantly during resting and refuelling periods on stop-over sites. Therefore, changes along the migration route can have severe impact on the birds' reproductive performance and eventually on population dynamics. Thus, we need a tool that integrates changes on individual sites along the flyway, estimates their consequences for migratory success and eventually for population dynamics of the focal species. Optimal migration models have already proved useful for providing general insights on the migrations of shorebirds, but could not be linked to particular migration systems, due to the lack of estimates for important parameters. Among these "parameters", the so-called terminal reward function is of paramount significance because this function links conditions encountered on stop-over sites and during the migratory journey to reproductive success and survival and establishes therefore a currency to evaluate consequences of individual decision.

In short, the aim of the model (called DYNAMIG) that was further developed in this project, is to provide a tool for effective management and policy making with regard to the aforementioned international obligations.

At present, DYNAMIG simulates the spring migration of individual birds. Based on species characters and the availability and quality of staging sites, it predicts the optimal migration schedule and the ensuing date and body condition upon arrival in the breeding area and the associated reproductive success. It also predicts the probability of dying during northward migration from starvation or predation.

Previous work on shorebirds indicated a noticeable absence of knowledge on the relationship between time and condition at arrival and subsequent reproductive success. Yet, this so-called terminal reward is of great importance in the calculation

of the optimal migration decisions. The current project therefore aimed at improving knowledge of model parameters, in particular the terminal reward function. The first step was to organise expeditions to the high arctic breeding grounds. The expedition results have already been published (Tulp *et al.* 2000; Tulp & Schekkerman 2001; Schekkerman *et al.* 2004). In this report we take the second step, namely to use the findings of the expeditions to estimate the model parameters and investigate if the parameterized model successfully described the migration of the shorebird species for which the model was parameterized. During the process, it became necessary to modify the model as well.

Initially, we intended to fully parameterize the model for seven different shorebird species: the Knot *Calidris canutus*, the Dunlin *Calidris alpina*, the Curlew Sandpiper *Calidris ferruginea*, the Little Stint *Calidris minuta*, the Sanderling *Calidris alba*, the Turnstone *Arenaria interpres* and the Grey Plover *Pluvialis squatarola*. We collected information on the migration routes of all seven species. It turned out that the best information was available for the Knot and this was also true for other important parameters, like energy expenditure. We subsequently focused our work on this species. As a result, a major part of the report consists of the derivation of parameter estimates of energetic costs, risk of predation and reproductive success for the two subspecies of Knot (*C.c. islandica* and *C.c. canutus*) on the basis of data collected as part of this project, or published in the literature.

On the basis of data collected during expeditions as part of this project, we succeeded in deriving a function for the terminal reward (the fitness payoff to birds that arrive on the breeding grounds on a certain date with a certain body condition) using an indirect approach. Growth of shorebird chicks was found to depend on insect availability and insect availability was found to depend on temperature, season and “depletion” (when the weather has been favourable for several days in a row it appears that the pool of insects that can emerge is “depleted”). This relationship allowed us to reconstruct the feeding conditions for the chicks on the basis of past weather data and calculate for each arrival time the number of chicks the bird could expect to fledge. To complete the picture, we also estimated the risk of starvation for a given arrival mass and a given arrival time, as well as the future reproductive success for adult birds that survived the breeding season. Our empirical investigations were focused on Taimyr, but we extrapolated the results to Greenland. To feel more secure about this kind of extrapolation, measurements on weather, insect availability and chick growth are needed for a variety of shorebird species on a range of locations spread over the entire arctic.

Once the parameters of the spring migration model have been estimated, the model can be used via forward simulations to make predictions on the following aspects of the migration schedule:

- The pattern of site use, i.e. which sites are used and which sites are skipped (migration route)
- The timing of site use, i.e. when do the birds arrive and when do they depart from the sites that are included in the migration schedule
- Arrival mass and departure mass at each stopover site

- Timing and condition at arrival on the breeding grounds
- The proportion of birds that die on migration
- The proportion of birds that survive, but fail to reach the breeding grounds
- The reproductive success achieved on the breeding grounds

We tested if the pattern of site use was correctly predicted by the model. In general, migration routes were correctly predicted, but there were also notable discrepancies, especially for the subspecies *canutus*. (1) Knots of the subspecies *canutus* wintering in South Africa probably migrate in a single leap to Guinea-Bissau, but the model Knots could not reach Guinea-Bissau in a single leap, (2) Knots of the subspecies *canutus* migrating northward from the Banc d'Arguin usually fly to the Wadden Sea in a single leap, but the model Knots always landed in France, (3) Knots of the subspecies *canutus* migrating northward from the Wadden Sea are believed to fly directly to their Siberian breeding grounds, but the model Knots always landed in northern Norway. It could be that our estimates of flight costs are too high, but we think this unlikely. Instead, the Knots probably rely on tailwinds. Including realistic (and thus variable) wind conditions will probably solve this problem.

The simulation results for the migration schedule of the Knot subspecies *islandica*, which breeds on Greenland and northern Canada and winters in NW Europe, were especially encouraging. The majority of this population uses Iceland as a stopover site, but a minority (20-30%) migrates via northern Norway. A sensitivity analysis indicated that birds breeding in the more westerly parts of the Canadian breeding range should migrate via Iceland, whereas the birds breeding on Greenland should migrate via northern Norway. At present, there are insufficient data to test this prediction.

We also tested if the timing of site use was correctly predicted. Forward simulations showed that the birds arrived on time. However, the birds departed too early from the wintering sites and migrated too slowly. This was true for all combinations of starting location and breeding area. Several possible explanations for this discrepancy exist. Our current model may overestimate the attractiveness of northerly sites early in the season. Alternatively, the costs of fattening quickly, which consist of increased predation risk, may be overestimated.

A sensitivity analysis of survival rates showed that survival rates predicted by the model generally varied between 90-100%. Quantitative tests of this prediction are not possible at present, but these survival figures seem reasonable for a long-lived species like the Knot.

We are encouraged by the progress that we made with regard to the application of DYNAMIG to the migrations of geese and swans (Beekman *et al.* 2002; Klaassen *et al.* 2006; Bauer *et al.* 2005) and shorebirds (this report), even if there are still details that do not fit. For Knots we are now in a good position to repeat the general calculations of Weber *et al.* (1999) on the effects of habitat loss or habitat degradation at migratory stopover sites. It is also possible to use the model to study some of the effects of climate change. Global climate change may affect migratory shorebirds

both in their winter and migration stopover sites (sea level rise, availability of intertidal habitats), during the migratory flights (wind conditions) and in the breeding range (climatic breeding conditions, vegetation belts). Clearly, some of these effects, like the effects of variable wind conditions, are not yet included in the model.

We end the report with the following recommendations:

- Test the prediction that Knots breeding in Canada migrate via Iceland and that Knots breeding in Greenland migrate via Norway
- Investigate if our method to construct the terminal reward from weather data can also be applied to other areas in the arctic and to other shorebird species
- Improve the spring migration model (DYNAMIG) by
 - Proper inclusion of variable wind conditions *en route*
 - Obtaining better empirical estimates of predation risk
 - Proper inclusion of seasonal changes in prey availability and prey quality
- Parameterize the spring migration model for other shorebird species
- Use the spring migration model for scenario calculations on the effects of climate change and habitat degradation on stopover sites
- Extend the spring migration model to the full annual cycle and include density dependence to allow predictions on population effects

Nederlandse Samenvatting

Een belangrijk deel van de steltlopers die gebruik maken van het waddengebied, zijn steltlopers die over lange afstanden trekken. Zulke lange-afstand trekkers zijn afhankelijk voor hun overleving van een keten van wadgebieden, ook wel aangeduid als *wetlands*. Omdat *wetlands* sterk worden bedreigd hebben veel landen, waaronder Nederland, internationale verdragen ondertekend om de *wetlands* te beschermen: de Ramsar conventie, de Europese Vogelrichtlijn, de Europese Habitatrichtlijn, Natura 2000, de biodiversiteits conventie, de diversiteit strategie van de Europese gemeenschap, de Bonn conventie en de Afrikaans Euraziatische watervogel overeenkomst. Effectieve bescherming vereist gereedschap om de gevolgen voor de vogels van habitat verlies en habitat verandering langs de trekweg in te schatten.

Voor arctisch broedende trekvogels is de *timing* van de activiteiten (zoals trek, broeden en ruien) van speciaal belang, omdat ze precies moeten samenvallen met de juiste condities in hun sterk in de loop van het seizoen variërende omgeving. Dit geldt met name voor de voorjaars trek naar de broedgebieden, wat een zeer kritische periode is in de jaarcyclus. Omdat er op de arctische toendra maar zeer kort tijd is om een broedsel groot te brengen zijn de datum en de toestand van aankomst van doorslaggevend belang en die zullen dan ook een sterk verband hebben met de fitness van de arriverende trekvogel. Wanneer en in welke conditie een vogel in het broedgebied arriveert zal in sterke mate afhankelijk zijn van de omstandigheden tijdens de trektocht en met name gedurende de rust- en opvetperiodes op de stopplaatsen. Dat betekent dat verandering onderweg een groot effect kunnen hebben op het broedsucces van de arctisch broedende trekvogels en daarmee uiteindelijk ook op de populatie-ontwikkelingen. Het zou zeer nuttig zijn als we de effecten van allerlei veranderingen langs de trekweg konden “sommen” en de gevolgen konden berekenen voor het succes tijdens de trek uiteindelijk voor de populatie dynamica van de soort. Optimale trekmodellen hebben hun nut bewezen bij het verkrijgen van algemene inzichten over de effecten van habitat verandering langs de trekweg. Tot op heden ontbrak de mogelijkheid om specifieke bedreigingen te onderzoeken. Dat was een gevolg van het feit dat belangrijke soortspecifieke parameters niet bekend waren. In het geval van de arctisch broedende steltlopers was er weinig tot niets bekend over de *terminal reward*; het verband tussen *timing* en conditie bij aankomst en het daaropvolgende broedsucces. Zonder een goede schatting van deze functie is het niet mogelijk om door te rekenen wat de gevolgen zijn van beslissingen tijdens de trek op het uiteindelijke broedsucces.

Een belangrijk doel van dit onderzoek was daarom om een goede schatting voor de *terminal reward* bij arctisch broedende steltlopers te krijgen om zodoende het optimale trekmodel DYNAMIG geschikt te maken voor onderzoek naar de meest effectieve manier om de arctische broedende steltlopers te beschermen. DYNAMIG simuleert de voorjaars trek van individuele vogels. Afhankelijk van de eigenschappen van een bepaalde soort trekvogel en de beschikbaarheid en kwaliteit van doortrekgebieden, berekent het model de optimale trekweg, inclusief data van aankomst en vertrek, de

bijbehorende veranderingen in conditie, het aankomstgewicht en de aankomstdatum en het daaruit voortvloeiende broedsucces. Het model voorspelt ook de kans om tijdens de trek naar het noorden om te komen als gevolg van verhongering of predatie.

Doel van dit project was om een aantal belangrijke parameters te schatten en zodoende DYNAMIG toepasbaar te maken voor arctisch broedende steltlopers. Omdat er zo weinig bekend was over de *terminal reward* bij arctisch broedende steltlopers vormde het schatten van deze functie een belangrijk onderdeel van het project. Om te beginnen werden een aantal expedities georganiseerd naar de hoognoordelijke broedgebieden in Siberië. Over de resultaten van die expedities is al uitvoerig gerapporteerd (Tulp *et al.* 2000; Tulp & Schekkerman 2001; Schekkerman *et al.* 2004). Dit rapport gaat over de tweede stap: het op basis van de expeditie gegevens schatten van de modelparameters en onderzoeken of het geparameteriseerde model in staat is de trekweg te voorspellen van de onderzochte soorten. Al doende bleek dat het nodig was het model op een aantal punten aan te passen.

Oorspronkelijk was het de bedoeling om het model voor zeven soorten steltlopers zo goed mogelijk te parameteriseren: de Kanoetstrandloper *Calidris canutus*, de Bonte Strandloper *Calidris alpina*, de Krombekstrandloper *Calidris ferruginea*, de Kleine Strandloper *Calidris minuta*, de Drieteenstrandloper *Calidris alba*, de Steenloper *Arenaria interpres* en de Zilverplevier *Pluvialis squatarola*. Voor alle soorten zijn we begonnen met het verzamelen van informatie over de trekweg. Daarbij bleek dat veruit de beste informatie beschikbaar was voor de Kanoetstrandloper en dat gold ook voor andere parameters, zoals de energie uitgave. Daarop werd besloten het model eerst toe te passen op de soort met de beste gegevens. Als gevolg daarvan bestaat dit rapport voor een belangrijk deel uit de afleiding van parameter waarden van de energie uitgave, predatie risico en broedsucces voor de twee ondersoorten van de Kanoetstrandloper (*C.c. islandica* and *C.c. canutus*), op basis van gegevens verzameld als onderdeel van dit project, of op basis van de literatuur.

Op basis van de als onderdeel van dit project uitgevoerde expedities naar het broedgebied waren we in staat een goede schatting te maken van de *terminal reward*. Het lukte niet om direct een verband te leggen tussen de *fitness payoff* en de datum van aankomst in het broedgebied en conditie bij aankomst, omdat het moeilijk was om vogels te vangen direct na aankomst en omdat een belangrijke deel van de weinige vogels die werden gevangen later niet terug werden gezien. Via een indirecte benadering hadden we echter wel succes. De groei van steltloperkuikens bleek af te hangen van de beschikbaarheid van insecten en de beschikbaarheid van insecten bleek af te hangen van temperatuur, seizoen en “uitputting” (als het weer een aantal dagen gunstig was geweest bleken er nauwelijks meer nieuwe insecten actief te worden). Op basis van deze relaties konden we middels historische weergegevens een verwachte groeisnelheid van de kuikens (en daarmee het broedsucces) uitrekenen voor elke aankomstdatum. Vroeg arriverende vogels lopen het risico een bevroren toendra te vinden en als ze dan te weinig reserves hebben is een wisse hongerdood hun lot. Op basis van de historische weergegevens konden we ook uitrekenen hoe

groot dit risico was afhankelijk van aankomstdatum en aankomstgewicht. Tot slot berekenden we hoeveel jongen een steltloper naar verwachting nog groot kan brengen in zijn verdere leven als het broedseizoen wordt overleefd. Ons empirisch onderzoek beperkte zich tot Taimyr in Siberië, maar we konden onze resultaten extrapoleren naar Groenland. Om meer zekerheid te krijgen dat dergelijke extrapolaties juist zijn, is het belangrijk om op een groot aantal locaties in het arctische gebied getallen te verzamelen over het weer, de beschikbaarheid van insecten en kuikengroei voor een groot aantal soorten steltlopers.

Het geparameteriseerde model kan gebruikt worden om via “voorwaartse simulaties” voorspellingen te doen over verschillende onderdelen van een trekweg:

- Gebruik van doortrekgebieden: welke gebieden worden aangedaan en welke gebieden worden overgeslagen?
- *Timing* van de trek: wanneer komen ze aan en wanneer vertrekken ze weer?
- Aankomstgewicht en vertrekgewicht in elk doortrekgebied
- Tijdstip van aankomst en conditie bij aankomst in het broedgebied
- Het percentage dieren dat sterft tijdens de voorjaarstrek
- Het percentage dieren dat er niet in slaagt het broedgebied te bereiken
- Het broedsucces

Een deel van deze voorspellingen kon worden getoetst.

Allereerst onderzochten we de voorspellingen over de trekroute. In het algemeen werden de trekroutes goed voorspeld, maar er waren uitzonderingen, met name voor de ondersoort *canutus*: (1) Kanoeten van deze ondersoort die in Zuid-Afrika overwinteren vliegen waarschijnlijk in één keer naar Guinee-Bissau, maar dat bleek voor de modelvogels niet mogelijk, (2) Kanoeten van deze ondersoorten vliegen meestal in één keer van de Banc d'Arguin naar de Waddenzee, maar de modelvogels maakten altijd een tussenstop in Frankrijk, (3) Er wordt aangenomen dat de Kanoeten van deze ondersoort zonder tussenstop van de Waddenzee naar hun Siberische broedgebieden vliegen, maar de modelvogels maakten altijd een tussenlanding in het noorden van Noorwegen. Er zijn verschillende verklaringen mogelijk. Misschien is de door ons gehanteerde schatting van de vlieggkosten te hoog. Dit lijkt onwaarschijnlijk. Het is aannemelijk dat de Kanoeten tijdens de trek gebruik maken van rugwinden. Dit probleem kan daarom waarschijnlijk worden opgelost door realistische (en dus ook variabele) wind condities in het model op te nemen.

De simulaties van de trekroute van de ondersoort *islandica*, die op Groenland en in het noorden van Canada broedt, waren met name bemoedigend. Het grootste deel van deze populatie gebruikt IJsland als tussenstation, maar een kleiner deel (20-30%) trekt via het noorden van Noorwegen naar de broedgebieden. Uit een gevoeligheidsanalyse bleek volgens het model dat vogels die in de westelijke delen van het Canadese broedgebied broeden via IJsland zouden moeten trekken, terwijl de vogels die op Groenland broeden via Noorwegen zouden moeten trekken. Op dit moment zijn er geen gegevens waarmee deze voorspelling getoetst kan worden.

Het voor Kanoeten geparameteriseerde model werd ook gebruikt om na te gaan of de *timing* van de trek correct werd voorspeld. Uit voorwaartse simulaties bleek dat de vogels op tijd in het broedgebied arriveerden. Echter, de vogels gingen te vroeg weg uit de overwinteringsgebieden en deden te lang over de trektocht als geheel. Dit gold voor alle combinaties van overwinteringsgebied en broedgebied. Er zijn verschillende verklaringen mogelijk. Misschien worden op dit moment de opvetmogelijkheden vroeg in het seizoen in de noordelijke gebieden overschat. Een andere mogelijkheid is dat de kosten van snel opvetten, bestaande uit een verhoogd predatierisico, worden overschat.

Uit een gevoeligheidsanalyse bleek dat de overleving varieerde tussen 90 en 100%. Een kwantitatieve toetsing van deze voorspellingen is op dit moment niet mogelijk, maar dergelijke overlevingsgetallen lijken realistisch voor een langlevende soort als de Kanoetstrandloper.

Al met al is er in de afgelopen jaren grote vooruitgang geboekt in het toepassen van het model DYNAMIG op de trekbewegingen van ganzen en zwanen (Beekman *et al.* 2002; Klaassen *et al.* 2006; Bauer *et al.* 2005) en steltlopers (dit rapport), ook al zijn er details die niet kloppen. Het is nu mogelijk om voor de Kanoetstrandloper de berekeningen van Weber *et al.* (1999) te herhalen over de effecten van habitat verlies en habitatverslechtering op de doortrekgebieden. Ook is het mogelijk het model te gebruiken om een aantal gevolgen van klimaatverandering door te rekenen. Klimaatverandering kan op verschillende manier effect hebben op de trekkende steltlopers. Zeespiegelstijging kan het oppervlakte wadplaten verkleinen dat als voedselgebied dient in de overwinteringsgebieden en de doortrekgebieden. Veranderingen in het weer, met name de windcondities, zullen effect hebben tijdens de lange vliegtochten. Temperatuurstijgingen zullen effect hebben op het voedselaanbod en het habitat (verschuivende vegetaties) in het broedgebied.

Het rapport eindigt met de volgende aanbevelingen:

- Toetsen van de voorspelling dat Kanoeten die in Canada broeden vooral via IJsland trekken en dat Kanoeten die op Groenland broeden vooral via Noorwegen trekken
- Onderzoeken of onze methode om de *terminal reward* te reconstrueren met behulp van weergegevens ook kan worden toegepast in andere arctische gebieden en op andere steltlopersoorten
- Verder verbeteren van het model over de voorjaarstrek (DYNAMIG) door:
 - Inbouwen van variabele windcondities *en route*
 - Verkrijgen van betere empirische schattingen van predatie risico's
 - Inbouwen van seizoensveranderingen in prooibeschikbaarheid
- Het model over de voorjaarstrek parameteriseren voor andere steltlopersoorten
- Het model gebruiken voor scenario berekeningen over effecten van klimaatveranderingen en aantasting van doortrekgebieden
- Uitbouwen van het model tot een model over de hele jaarcyclus waarin ook dichtheidsafhankelijkheid zit zodat populatievoorspellingen mogelijk worden

1 Introduction

Shorebirds are prominent long-distance migrants and depend on a chain of wetlands for their survival. For the shorebirds that breed on the tundra from eastern Canada to western Siberia and winter in Africa, the Wadden Sea is an extremely important staging site (Figure 1-1). Wetlands are a threatened habitat and many countries, including the Netherlands, have signed international agreements to protect these wetlands, e.g. the Ramsar Convention, European Birds Directive, European Habitats Directive, Natura 2000, The Convention on Biological Diversity, European Community Diversity Strategy, Bonn Convention and the African Eurasian Waterbird Agreement. In many cases, the ministry of LNV is in charge of the obligations that follow from these treaties. Effective protection requires a tool to assess the consequences of habitat loss and habitat change along the migration route. The aim of the model that was further developed in this project, is to provide a tool for effective management and policy making with regard to these international obligations. Before explaining what we may expect from such a tool, we need to describe migratory flyways in some more detail.



Figure 1-1: Picture of the Wadden Sea as a vital link in the chain of wetlands linking the arctic breeding grounds of many shorebird species to the two major wintering grounds in Africa, the Banc d'Arguin in Mauritania, and the Archipelago dos Bijagos in Guinea-Bissau. From van de Kam et al. (2004).

Migratory flyways are networks of staging sites connecting breeding and wintering areas of migratory birds. Central to the conservation of flyways is the principle that migratory birds depend on the existence of a chain or network of areas visited over the course of the annual cycle. Each site is important in itself, but the functioning of sites is also

influenced by the quality of other sites in the chain (Piersma 1987; Alerstam 1990; Ens *et al.* 1994). For effective conservation and management of migratory populations, the functional links between sites within these networks need to be elucidated. To this end, this project aimed to improve the dynamic migration model DYNAMIG, developed within the framework of the National Programme on Climate Research NOP I and II (Ens *et al.* 1995; Weber *et al.* 1998; Weber *et al.* 1999; Klaassen & Ens 2001). The model DYNAMIG provides a theoretical basis for the concept of site networks, and generates predictions of the consequences of changes in the quality of sites within the network using stochastic dynamic programming (McNamara & Houston 1986; Mangel & Clark 1986; Mangel & Clark 1988; Houston & McNamara 1999). These changes in site quality may be climate-related, human-induced or both. The model can also help identify sites of special importance to the functioning of the network, which deserve conservation priority.

For an Arctic breeding migrant, the timing of activities (e.g. migration, breeding, moult) poses a particular challenge since these should be synchronized with appropriate conditions in their highly seasonal environments. This notably applies for the spring migration to the breeding grounds, which is generally believed to be one of the most sensitive parts of the annual cycle. Time of and state at arrival on the breeding grounds are likely correlates of a migrants' fitness since the time available for reproduction is restricted (Drent & Daan 1980; Alerstam 1990; Ens *et al.* 1994; Clark & Butler 1999; Kokko 1999; Prop *et al.* 2003). Therefore, changes along the migration route can have severe impact on the birds' reproductive performance and eventually on population dynamics (Weber *et al.* 1999; Both & Visser 2001; Forchhammer *et al.* 2002; Gordo *et al.* 2005). However, when and in which state birds arrive on the breeding grounds highly depends on conditions encountered during migratory flights and more importantly during resting and refuelling periods on stop-over sites. Thus, only with a model that integrates changes on individual sites along the flyway, is it possible to estimate the consequences of these changes for migratory success and eventually for population dynamics of the focal species.

At present, DYNAMIG simulates the spring migration of individual birds. Based on species characters and the availability and quality of staging sites, it predicts the optimal migration schedule and the ensuing date and body condition upon arrival in the breeding area and the associated reproductive success. It also predicts the probability of dying during northward migration from starvation or predation. In 1997, a workshop was organised to put the model to the test, i.e. it was investigated to what extent the model succeeded in predicting current migration schedules for well-studied migration systems of geese and shorebirds (Klaassen & Ens 2001). It was concluded that:

1. The model in its current form appeared not to be applicable to a minority of species, such as the Pectoral Sandpiper, which does not make use of a number of clearly localised intermediate locations.
2. For some species, the parameter estimates lead to nonsensical results, but it appeared practically certain that this was due to faulty parameter estimation.
3. The simulations were encouraging for a fairly large number of species.

Apart from being encouraging, the workshop also demonstrated a clear absence of knowledge on important parameters and relationships. For shorebirds, there was a noticeable absence of knowledge on the relationship between time and condition at arrival and subsequent reproductive success, also known as the terminal reward. The current project therefore aimed at improving knowledge of model parameters, in particular the terminal reward function. The first step was to organise expeditions to the high arctic breeding grounds in 2000 (Tulp *et al.* 2000), 2001 (Tulp & Schekkerman 2001) and 2002 (Schekkerman *et al.* 2004). The second step was to use the findings to estimate the model parameters and investigate if the parameterized model successfully described the migration of the shorebird species for which the model was parameterized. During the process, it became necessary to modify the model as well.

Initially, we intended to fully parameterize the model for seven different shorebird species: the Knot *Calidris canutus*, the Dunlin *Calidris alpina*, the Curlew Sandpiper *Calidris ferruginea*, the Little Stint *Calidris minuta*, the Sanderling *Calidris alba*, the Turnstone *Arenaria interpres* and the Grey Plover *Pluvialis squatarola*. We collected information on the migration routes of all seven species. It turned out that the best information was available for the Knot and this was also true for other important parameters, like energy expenditure. In no small measure, this is the result of the many investigations of Theunis Piersma and his co-workers (Piersma 1994; van Gils 2004). We subsequently focused our work on this species. This proved to be so much work that it took all the time we had available during the last year of the project.

Having described the history and the aim of the project, we briefly describe the contents of the chapters that follow. In chapter 2 we describe the model. We pay special attention to those parts of the model that differ from the original formulation of Weber *et al.* (1998) and our arguments for making these changes. In the next four chapters we describe how we arrived at estimates for the various parameters on the basis of our own studies and data in the published literature. Chapter 3 deals with the migration routes and the pattern of mass gain, not only for Knot, but also for the other selected shorebird species. Chapter 4 deals with energetics, including basal metabolic rate, maintenance metabolism and daily existence energy, the costs of fuelling and flying and an estimate of flight range. These topics are well studied for Knots. Chapter 5 deals with the risk of predation, a topic on which we have very little quantitative information for Knots (or any of the other selected shorebird species for that matter), so that we decided to review the theory and the empirical data for birds in general. Chapter 6 shows how we estimated the terminal reward function for Knots breeding in Greenland (subspecies *islandica*) and Knots breeding in Siberia (subspecies *canutus*). Having parameterized the model, we used it to simulate the migration schedule in chapter 7. We compare the model results with what we know of the migration schedules of the two subspecies of Knot. We also investigate how sensitive the model results are to variations in the parameter estimates. Next, we discuss the results in chapter 8 and in chapter 9 we end the main body of this report with recommendations for future investigations.

2 Model description

We used dynamic programming to find the sequence of migratory decisions that would maximise the fitness of shorebirds under the environmental conditions encountered during spring migration (McNamara & Houston 1986; Mangel & Clark 1986; Mangel & Clark 1988; Houston & McNamara 1999). The dynamic program that we use was developed by Weber *et al.* (1998). The original model was roughly parameterized for a shorebird with the size of a Knot and used for a theoretical investigation of the consequences of habitat change at the wintering site and various stopover sites (Weber *et al.* 1999). Subsequently, the model was slightly modified and parameterized to study the migrations of Bewick's Swans *Cygnus bewickii* (Beekman *et al.* 2002) and Pink-footed Geese *Anser brachyrhynchus* (Bauer *et al.* 2005). For the current study, the model was extensively modified and much effort was invested to obtain the best possible estimates for each of the parameters. For reasons explained in chapter 1, we parameterized the model for the two subspecies of the Knot that depend on the Wadden Sea for their survival, i.e. subspecies *islandica*, which breeds on Greenland and the eastern Canadian arctic, and subspecies *canutus*, which breeds in western Siberia.

We distinguished potential sites i ranging from the wintering grounds to the breeding grounds (see Chapter 3 for site locations and distances between sites). The migration period was divided into whole days t covering the period from 1st February to 31st July, i.e. 180 days.

We assumed that at time t , the expected future fitness F of a female shorebird, is a function of its fuel stores x , and its location i : $F(x,t,i)$. Body stores x may vary between 0, where the bird used in our simulations reaches a body mass of 110 g and dies of starvation, and x_{\max} , where it reaches the maximum fuel load at a body mass of 210 g. At the breeding or destination site N , the expected future fitness is $F(x,t)$. For each time step when the bird has not yet arrived at its destination, it has two behavioural options: either foraging at intensity u ($0 \leq u \leq 1$) or, if fuel stores permit, flying to another site.

With the dynamic programming equations presented below, a matrix is compiled containing the optimal behavioural decisions for all combinations of fuel stores, times and sites. This decision matrix allows us to follow the fate of individual birds during their migratory journey, i.e., the timing and intensity of use of the various sites along the migration route.

Expected fitness in terms of young produced at the destination ($i = N$) and in future years is a function of arrival date, state upon arrival and the expected fitness from future breeding attempts. The expected fitness at the destination ($i=N$) has been determined by the expected production of young in the current breeding season, $R(t)$, the survival prospects, $S(x,t)$, and the fitness gain from future breeding attempts, B_0 .

$$F(x,t,N) = S(x,t).R(t) + B_0 \quad (2.1)$$

In chapter 6 we describe the derivation of this relationship from empirical studies. Here, we provide a brief summary of that derivation. The first problem that a bird arriving on the tundra may encounter is that the tundra is still covered with snow. In that case the bird cannot feed and has to rely on the fuel stores that remain after the migratory journey. Clearly, the higher the stores, the greater the likelihood that the bird will survive this critical period. Also, the probability of encountering snow decrease in the course of the season (until fall, when the risk increases again). This leads to a sigmoidal function for $S(x,t)$, the probability of surviving to breed, given arrival mass x and arrival time t . The shape of this function is determined by three empirically defined constants s_0 , s_1 and s_2 :

$$S(x,t) = \frac{\exp[-s_0 + s_1 t + s_2 x]}{1 + \exp[-s_0 + s_1 t + s_2 x]} \quad (2.2)$$

The second problem is that there is only a rather narrow time window during which insects are sufficiently abundant to provide good feeding conditions for the chicks. The laying of the eggs must be such that the growing period of the chicks coincides with the period of maximal insect abundance. Since egg laying starts very quickly after arrival, the number of chicks that will fledge is related to arrival date by a bell-shaped curve. The exact shape of this curve is determined by three empirically defined constants, α_0 , α_1 and α_2 :

$$R(t) = \alpha_0 \cdot \exp\left[\frac{-(t - \alpha_1)^2}{\alpha_2^2}\right] \quad (2.3)$$

If the female and its mate are unable to complete their migratory journey successfully the females expected fitness equals B_0 . To resemble the approximated average life-time reproductive success of females in a stable population, B_0 was set to 3.

The maximum intake rate that a foraging shorebird may attain is site and time dependent ($g(i,t)$, kJ/d). The actual intake rate is determined by the foraging intensity u . How much of this intake rate ultimately is stored as body stores depends on the energy expenditure $e(i, t)$, (kJ/d). Maintaining fuel stores incurs a fitness cost in terms of increased risks of predation and injury (Witter & Cuthill 1993). Additionally, foraging with a certain intensity bears also a predation risk. Thus, the total predation risk contains three parts:

$$m(x,u,i) = m_0(i) + m_\gamma(i) \cdot u^{a_1} + m_\beta(i) \cdot x^{a_2} \quad (2.4)$$

Where $m_0(i)$ is the site-specific baseline predation risk, $m_\gamma(i) \cdot u^{a_1}$ is the foraging intensity (u) dependent risk, and $m_\beta(i) \cdot x^{a_2}$ the fuel-stores (x) dependent predation risk.

If the bird decides to forage, it should forage with an intensity u that yields the maximum expected fitness at the destination:

$$H_f(x,t,i) = \max_u [(1 - m(x,u,i)) F(x + ug(t,i) - e(t,i), t+1, i)] \quad (2.5)$$

Alternatively, an individual can depart to the next site depending on its fuel stores x and the distance D (km) to the destination site. Its fuel stores upon arrival at the destination x_a were calculated using

$$x_a = \left(\frac{c^2}{(c - (c(1 - (1 + x/x_{\max})^{-0.5} - D))^2 - 1} \right) \cdot x_{\max} \quad (2.6)$$

where c is a flight range parameter which is calculated using

$$c = \frac{D_{\max}}{1 - (x_f / x_{\max})^{-0.5}} \quad (2.7)$$

and D_{\max} is the maximum flight range when dedicating fraction x_f of the maximum fuel load x_{\max} to flight. For the shorebirds in this study we used $x_f = x_{\max}$. We calculated D_{\max} by dividing the maximum fuel load by the flight costs f in terms of energy (Kvist *et al.* 2001):

$$D_{\max} = \frac{x_{\max}}{f} \quad (2.8)$$

If an individual decides to depart, it should fly to the site j yielding the maximum expected fitness at the destination:

$$H_d(x, t, i) = \max_j [F(x_a, t + (\sum_{z=i}^{j-1} D_z / v), j)] \quad (2.9)$$

where v is flight speed, which was estimated at 1440 km/d.

The optimal decision is the behavioural alternative, foraging or departing, yielding the highest future expected reproductive success:

$$F(x, t, i) = \max[H_f(x, t, i), H_d(x, t, i)] \quad (2.10)$$

For computational reasons x , t , and i must be whole numbers.

The optimal decision matrix for all combinations of time, site and body reserves will be used in subsequent forward simulations and thus allow us to track birds during their spring migration. Consequently, we can predict staging times and body reserve dynamics from these simulations and compare the predicted values with empirical data.

3 Migration routes and mass gain

The Great Circle Mapper developed by Karl L. Swartz (<http://gc.kls2.com>) yielded the shortest distances between staging sites and allowed the drawing of maps of the various stopover sites, with lines connecting the sites.

3.1 Red Knot *Calidris canutus islandica* (N-Canada & Greenland)

The paper by (Davidson & Wilson 1992) is the primary source for migration routes and sites.

Table 3-1: Migration routes and sites.

Site	Lat-long	Numbers	Arrival	Departure	Source
<i>Wintering areas</i>					
1 France, N-Brittany	49N 02W	27,000			(Stroud <i>et al.</i> 2004)
2 NL, Wadden Sea	53N 05E	90,000			(Stroud <i>et al.</i> 2004)
3 UK, Morecambe Bay, Wash	54N 02W	290,000			(Stroud <i>et al.</i> 2004)
<i>Spring staging sites</i>					
3 UK, Morecambe Bay, Wash	54N 02W			1-7 May	Mainly 1970s; (Davidson & Wilson 1992)
4 D, Schleswig-Holstein	54N 08E	300,000		1-15 May	(Davidson & Wilson 1992)
5 W Iceland	65N 23W	265,000	1-10 May	25 May – 2 Jun	(Davidson & Wilson 1992)
6 N Norway	70N 22E	50,000	1-10 May	25-29 May	(Davidson & Wilson 1992)
<i>Breeding Grounds</i>					
7 N Greenland / Canada	80N 70W		26 May – 7 Jun		

Table 3-2: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
1 France						No data
2 NL, Wadden Sea						No data
3 UK, Wash, Morecambe Bay	2.0	1.0	135	185-195	30	(Davidson & Wilson 1992)
3 UK, Wash	1.7	-	-	187	30	(Piersma <i>et al.</i> 2004)
4 D, Schleswig-Holstein	2.9	-	142	185-195	30?	(Prokosch 1988; Davidson & Wilson 1992)
4 D, Schleswig-Holstein	2.8	-	-	191	20	(Piersma <i>et al.</i> 2004) from (Prokosch 1988)
5 W Iceland	3.1	0.3	135-145	210	21	(Davidson & Wilson 1992; Alerstam <i>et al.</i> 1992; Gudmundsson <i>et al.</i> 1991)
5 W Iceland	2.9	-	-	211	28	(Piersma <i>et al.</i> 2004; Piersma <i>et al.</i> 1999; Gudmundsson <i>et al.</i> 1991)
6 N Norway	3.8	1.4	135-145	205-210	23	(Davidson & Wilson 1992)
6 N Norway	2.7	-	-	190	21	(Piersma <i>et al.</i> 2004) from (Davidson & Evans 1986)
8 NE Canada	-2.2	1.2	143-150			(Davidson & Wilson 1992)

Table 3-3. Distances between the sites considered as potentially useful to Icelandic Knots (*C. c. islandica*).

nr	Site	lat	long	2	3	4	5	6	7
1	N-Brittany	49N	02W	662	556	888	2169	2665	4259
2	Wadden Sea	53N	05E		477	228	2062	2082	3966
3	Morecambe Bay, Wash	54N	02W			655	1692	2150	3725
4	Schleswig-Holstein	54N	08E				2107	1917	3918
5	W Iceland	65N	23W					1950	2177
6	N Norway	70N	22E						2521
7	Greenland/Canada	80N	70W						



Figure 3-1: Wintering sites, stopover site and breeding location as well as distances between these sites for the Icelandic subspecies of the Knot *Calidris canutus islandica*.

3.2 Red Knot *Calidris c. canutus* (Taymir)

Table 3-4: Migration routes and sites.

Site	Lat-long	Numbers	Arrival	Depart	Source
<i>Wintering areas</i>					
1 South Africa	33S 18E	6,500	1 Apr	15-20 Apr	(Stroud <i>et al.</i> 2004; Piersma <i>et al.</i> 1992)
2 Guinea-Bissau	11N 16W	30,000		1 May	(Stroud <i>et al.</i> 2004; Piersma <i>et al.</i> 2004)
3 Mauritania	20N 17W	260,000	1 Apr	1-8 May	(Stroud <i>et al.</i> 2004; Piersma <i>et al.</i> 1990; Piersma <i>et al.</i> 1992)
<i>Spring staging sites</i>					
4 W France	46N 02W	0-30,000		12-20 May	Emergency site? (Piersma <i>et al.</i> 1992)
5 D, Schleswig-Holstein	54N 08E			2-9 June	(Piersma <i>et al.</i> 1992) 1 Jun (Piersma <i>et al.</i> 2004)
6 N-Norway	70N 22E	Few?			Some birds (Spaans, pers. comm.)
7 White Sea	65N 37E	None?			Importance unknown
<i>Breeding Grounds</i>					
8 Taymir Peninsula	75N 89E			7-20 June	

Table 3-5: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
1 South Africa	1.7					(Piersma <i>et al.</i> 1992) from (Summers & Waltner 1979)
1 South Africa	1.5	-	-	191	40	(Piersma <i>et al.</i> 2004) from (Summers & Waltner 1979)
2 Mauritania	0.7	-	-	168	60	(Ens <i>et al.</i> 1989; Piersma <i>et al.</i> 2004)
3 Guinea Bissau	0.9	-	-	157	70	(Piersma <i>et al.</i> 2004)
4 W France	?					No data
5 Wadden Sea	2.5 (3.6)					(Prokosch 1988)
5 Wadden Sea	3.0	-	-	210	28	(Piersma <i>et al.</i> 2004) from (Prokosch 1988)
8 Taymir	-	-	130			(Schekkerman <i>et al.</i> 2004)

Table 3-6: Distances between the sites considered as potentially useful to Siberian Knots (*C. c. canutus*).

nr	site	lat	long	2	3	4	5	6	7	8
1	South Africa	33S	18E	6061	6946	8978	9687	11426	10989	12996
2	Guinea-Bissau	11N	16W		1002	4101	5222	7072	7225	9254
3	Mauritania	20N	17W			3194	4331	6134	6350	8319
4	Western France	46N	02W				1140	2980	3159	5156
5	Schleswig-Holstein	54N	08E					1917	2019	4057
6	North Norway	70N	22E						845	2185
7	White Sea	65N	37E							2174
8	Taimyr Peninsula	75N	89E							

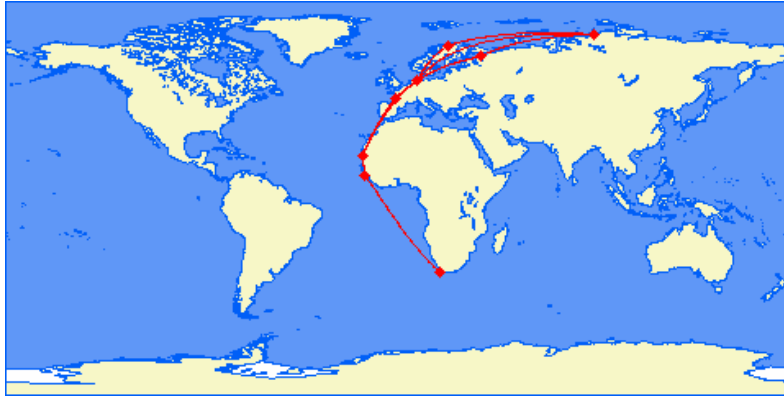


Figure 3-2: Wintering sites, stopover site and breeding location as well as distances between these sites for the Siberian subspecies of the Knot *Calidris canutus canutus*.

3.3 Dunlin – *Calidris alpina arctica* (Greenland)

For the subspecies *arctica* we found no useful data on patterns of mass gain in the literature. Most of the Dunlin wintering in Africa actually belong to the subspecies *schinzii*, which breeds on Iceland, Scotland and in the Baltic region. Since these breeding areas are outside the arctic region, we have not considered this subspecies in this report.

Table 3-7: Migration routes and sites.

Site	Lat-long	Arrival or start of mass gain
<i>Wintering areas</i>		
1 Mauritania	20N 17W	
2 Morocco	32N 10W	
<i>Spring staging sites</i>		
3 SW Portugal	39N 09W	
4 W France	47N 02W	
5 W Britain	54N 03W	
6 Hebrides	58N 07W	
7 SW Iceland	65N 23W	
<i>Breeding Grounds</i>		
8 NE Greenland	74N 23W	Early June

Table 3-8: Used routes and distances between sites

winter-early spring	D1-2 1550	D1-3 2240	D1-4 3290	D1-5 3960	D1-6 4300
	D2-3 780	D2-4 1800	D2-5 2500	D2-6 2900	
	D3-4	D3-5 1730	D3-6 2100		
early-late spring	D2-7 3800	D3-7 3030	D4-5 780	D4-6 1270	D4-7 2370
	D5-6 510	D5-7 1650			
late spring	D4-8 3180	D5-8 2400	D6-7 1150	D6-8 1910	D7-8 1000



Figure 3-3 Wintering sites, stopover site and breeding location as well as distances between these sites for the Greenland subspecies of the Dunlin *Calidris alpina arctica*.

3.4 Dunlin – *Calidris alpina alpina* (Yamal)

Note: about 50% of the Tunisia winter population is also *alpina* but migrates via route of *centralis* through Black Sea region; see there.

Table 3-9: Migration routes and sites.

Site	Lat-long	Numbers	Arrival	Departure	Source
<i>Wintering areas</i>					
1 UK	52N 00W				
<i>Spring staging sites</i>					
2 Wadden Sea	54N 07E		1 May	25 May	“Siberian” birds (Goede <i>et al.</i> 1990)
3 White Sea?	65N 37E				
<i>Breeding Grounds</i>					
4 Yamal	70N 70E				

Table 3-10: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
East England	0.53 (1.0)		55	74	50	<i>alpina</i> in May (Pienkowski <i>et al.</i> 1979)
Oosterschelde	1.0 (0.7)	0.4	-	70	-	(Meininger & van Swelm 1989)
W Wadden Sea	0.91		?	79	31	(Goede <i>et al.</i> 1990)

Table 3-11: Used routes and distances between sites (most-used in bold)

winter-breeding	D1-2 520	D1-3 2540	D1-4 3980	D2-3 2060	D2-4 3560
	D3-4 1500				



Figure 3-4: Wintering sites, stopover site and breeding location as well as distances between these sites for the nominate subspecies of the Dunlin *Calidris alpina alpina*.

3.5 Dunlin – *Calidris alpina centralis* (E Mediterranean – Taymir)

Note that about 50% of the population wintering in Tunisia consists of *alpina*, which migrates via route of *centralis* through Black Sea region.

Table 3-12: Migration routes and sites.

Site	Lat-long
<i>Wintering areas</i>	
1 Tunisia	34N 11E
2 Egypt	32N 32E
<i>Spring staging sites</i>	
3 N Greece	42N 25E
4 S Turkey	38N 36E
5 N Black Sea	47N 35E
6 White Sea?	65N 37E
<i>Breeding Grounds</i>	
7 Taymir	73N 80E

Table 3-13: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
Tunisia	(0.15)	-	-	-	-	From April to May and little synchronised fattening (Spiekman <i>et al.</i> 1993)
Egypt	low	-	52	57	-	(Meininger & Schekkerman 1994)
Israel	0?	-	-	46	-	Birds probably left without fattening (Keijl <i>et al.</i> 1992)
South Turkey	0?	-	-	-	-	No synchronised fattening observed (van der Have <i>et al.</i> 1988)
N Greece	(0.1)					April; no synchronous fattening
N Black Sea	0.87	0.07		65-75	18	(Chernichko <i>et al.</i> 1993)

Table 3-14: Used routes and distances between sites:

early spring	D1-3 1500	D1-5 2470	D3-5 970	D2-4 760	D2-5 1690
	D4-5 1000				
late spring	D1-6 3870	D3-6 2670	D4-6 3010	D5-6 2010	D5-7 3660
	D6-7 1880	D1-7 5750	D2-7 5300		



Figure 3-5: Wintering sites, stopover site and breeding location as well as distances between these sites for the Siberian subspecies of the Dunlin *Calidris alpina centralis*.

3.6 Curlew Sandpiper *Calidris ferruginea* (Africa – Taimyr)

Two routes mapped based on Taimyr recoveries from UK, Spain, S Africa: W-Africa-Tunisia-Black Sea (Western) and S-Africa-Rift Valley-Middle East (Southern). Forthcoming issue of International Wader Studies on Curlew Sandpiper Migrations, which is not yet published, should contain most of the needed information. Current evidence suggests that the Caspian region is only used in autumn and not used for stopover in spring, but this should be checked.

Table 3-15: Migration routes and sites.

Site	Lat-long	Numbers	Arrival	Departure	Source
<i>Wintering areas</i>					
1 Guinea-Bissau	11N 16W	327,000			(Stroud <i>et al.</i> 2004)
2 Mauritania	20N 17W	237,000			(Stroud <i>et al.</i> 2004)
3 South Africa	33S 18E	120,000		10 April	(Stroud <i>et al.</i> 2004), declining
4 East Africa	04S 40E	180,000		Late April	(Stroud <i>et al.</i> 2004)
<i>Spring staging sites</i>					
5 Kenya, Rift Valley	34N 11E	>10,000		Mid-May	
6 Persian Gulf	27N 56E	?			
7 Tunisia	34N 11E				
8 E Mediterranean (Egypt)	32N 32E	>20,000			
9 N Black Sea, Sivash	46N 35E	50,000			
10 Novosibirsk?	55N 77E	?			
<i>Breeding Grounds</i>					
11 Taimyr	74N 90E		8-20 June		

Table 3-16: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
South Africa	0.52		55	80	55	March (Elliot <i>et al.</i> 1976)
Guinea-Bissau	0.33		55	75-80	45	April (Wolff 1998)
Mauritania	0.48	-	-	73	-	April van Brederode in (Ens <i>et al.</i> 1989) and (Zwarts <i>et al.</i> 1990)
Tunisia	0	-	-	-	-	No synchronous fattening (Spiekman <i>et al.</i> 1993)
Egypt	0	-	-	76	-	(Meininger & Schekkerman 1994)
W Greece	0	-	-	-	-	(Cottaar <i>et al.</i> 1995)
N Greece	0.6 (1.0)	-	-	-	-	Recapture is for one individual only (de Nobel <i>et al.</i> 1990)
Persian Gulf, UAE	0.9	-	-	73	-	May (Keijl <i>et al.</i> 1998)
N Black Sea	-	-	-	56?	-	No gain observed; low masses (Chernichko <i>et al.</i> 1993)

Table 3-17: Used routes and distances between sites (most-used in bold)

Western route (W-Africa)	D1-2 970	D1-7 3720	D1-9 6150	D2-7 3170
	D2-9 5520	D7-9 2430	D9-11 4100	D7-11 6070
	D8-10 4330	D9-10 3090	D10-11 2200	
Southern route	D3-5 4500	D5-8 3130	D5-9 4660	D8-9 1580
	D8-11 5650	D9-11 4100		
	D3-4 3940	D5-6 3320	D6-11 5600	
	D6-10 3550	D8-10	D9-10 3090	D10-11 2200



Figure 3-6: Wintering sites, stopover site and breeding location as well as distances between these sites for the Curlew Sandpiper *Calidris ferruginea*.

3.7 Little Stint *Calidris minuta* (S/E Africa – Taimyr)

One route mapped based on Taimyr recoveries from Namibia, Tanzania, Israel and Persian Gulf; there are many other winter areas and routes!

Table 3-18: Migration routes and sites.

Site	Lat-long	Numbers	Arrival or start of mass gain	Departure	Source
<i>Wintering areas</i>					
1 Southern Africa	22S 15E				
2 E Africa Rift Valley	04N 36E				Dep?
<i>Spring staging sites</i>					
2 E Africa Rift Valley	04N 36E	?		Mid-May	
3 S Red Sea	12N 42E				
4 Egypt	32N 32E	?			
5 Turkey, inland lakes	38N 33E				
6 Persian Gulf	27N 56E	?			
7 N Black Sea, Sivash	46N 35E	?			
8 Omsk, Baraba steppe	54N 73E	?			Or change to Caspian Sea?
<i>Breeding Grounds</i>					
9 Taimyr	73N 80E		8-20 June		

Table 3-19: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
South Africa	0.32		21	50	33	April (Middlemiss 1961)
Kenya, Rift Valley	0.19 (0.23)		21	33	61	(Pearson 1987)
Mauritania	0.22	-	-	30	-	Fletcher in (Ens <i>et al.</i> 1989; Zwarts <i>et al.</i> 1990)
Tunisia	0	-	-	-	-	April, no gain observed, turnover? (Spiekman <i>et al.</i> 1993)
Egypt	0.31	0.13	25	35	?	April-May (Meininger & Schekkerman 1994)
Israel	0.13 (0.5)			35	-	(Keijl <i>et al.</i> 1992)
N Greece	(1.9)	0.4	-	-	-	April-May (de Nobel <i>et al.</i> 1990)
S Turkey	0?	-	-	-	-	In two studies no gain: high turnover? (van der Have <i>et al.</i> 1988; Kivit <i>et al.</i> 1994)
C Turkey	0.34			32	12	(Schekkerman & van Roomen 1993)
N Black Sea	0.5	-	-	-	-	(Chernichko <i>et al.</i> 1993)

Table 3-20: Used routes and distances between sites

Southern route	D1-2 3260	D2-3 1540	D2-4 3550	D4-5 670	D4-7	1720
	D5-7 1050					
	D2-6 3700	D3-4 2440	D3-6 2200			
	D6-8 3300	D6-9 5300	D7-8 2640	D7-9 3600	D8-9 2140	



Figure 3-7: Wintering sites, stopover site and breeding location as well as distances between these sites for those Little Stint *Calidris minuta* that breed on Taimyr and winter in Africa.

3.8 Sanderling *Calidris alba* (Greenland + Taimyr)

Picture not clear; literature suggests that both Nearctic and Palearctic Sanderlings mix and winter all along the coast from S Africa to Europe (Summers *et al.* 1987; Wymenga *et al.*

1990). Still IWS 15 distinguishes S-Africa/W-Asian populations from the W-Africa-Atlantic one.

Table 3-21: Migration routes and sites.

Site		Numbers
Wintering areas	West Africa	78,000
	Western Europe	42,000
	South Africa	98,000
	East Africa	26,000
Spring staging sites	England	
	Hebrides	
	SW Iceland	
Breeding Grounds	NE Greenland	
	NE Canada	

Table 3-22: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Period	Gain (g/d)	SD _{gain}	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
South Africa	April	0.52		47	85	73	(Summers <i>et al.</i> 1987)
Mauritania	April	0.36			64	40	Smit & van Spanje in (Ens <i>et al.</i> 1989)
Scotland	May	0.85		?	68	24	(Clark <i>et al.</i> 1982)
E England	May	0.99		?	85	38	(Davidson 1984)

3.9 Turnstone – *Arenaria interpres*

Table 3-23: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Period	Gain (g/d)	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
South Africa	April	1.0	100	165	65	(Summers <i>et al.</i> 1989)
Guinea-Bissau		0.71	-	160	60	(Wolff 1998)
Mauritania		0.7 (1.3)	100	140	31	(Ens <i>et al.</i> 1990)
Tunisia		1.1 (4.0)	-	-	-	Only one individual recaptured (Spiekman <i>et al.</i> 1993)
W England		1.5	?	160	40	(Zwarts <i>et al.</i> 1990) from (Clapham 1979)
Oosterschelde	April	0.5	-	-	-	(Meininger & van Swelm 1989)
Oosterschelde	May	2.9	-	160	-	(Meininger & van Swelm 1989)
Scotland		1.7	?	155	32	(Summers <i>et al.</i> 1989)
Iceland		2.1	?	160	29	(Morrison 1975)

3.10 Grey Plover – *Pluvialis squatarola*

Table 3-24: Mass gain at spring staging sites in gram per day. Estimates based on reweighing of individuals are in brackets.

Site	Period	Gain (g/d)	M _{arrive} (g)	M _{depart} (g)	Days fuelling	Source
South Africa		2.24	187	318	58	(Summers & Waltner 1979)
Guinea-Bissau		1.2	185	250	45	(Wolff 1998)
N Greece	April	(0.7)	-	-	-	(N=12) (de Nobel <i>et al.</i> 1990)
E England	May	3.37	?	318	39	(Branson & Minton 1976)
Oosterschelde	Apr-May	3.8	-	-	-	(Meininger & van Swelm 1989)
E Wadden Sea	May	3.6 (8.6)	?	333	20	(Prokosch 1988)

4 Energetic costs

This chapter describes the energetic costs of migration. Parameter estimates are for the Red Knot. Nomenclature of variables and parameters is provided in Table 4-1. If appropriate, an estimate that applies to Red Knots is given. The source of the estimate is explained in the sections below.

Table 4-1: Energetic parameters, the units in which the parameter (or variable) is measured, a verbal explanation or definition and an estimate for the Red Knot if appropriate.

Parameter or variable	units	explanation	Value for Red Knot
SMR	W	Standard Metabolic Rate	
BMR	W	Basal Metabolic Rate (SMR above lower critical temperature)	0.95
MMR	W	Maintenance Metabolic Rate, i.e. metabolic rate of postabsorptive birds resting or sleeping in different microhabitats; in the laboratory SMR=MMR	
DEE	W	Daily Existence Energy = MMR + costs activity + HIF (heat increment of feeding) + energy retention (storage) + costs of synthesis	
H_{sm}	W	Heat loss standard mount	
K_{esm}	W/ °C	Conductance of the standard mount in the standard environment, i.e. wind speed of 1 m/s	0.055
K_{es}	W/ °C	Conductance at a wind speed of 1 m/s of live birds	0.055
K_e	W/ °C	Convection-free conductance	0.045
K_u	W/ °C	Conductance at wind speed u	
K_r	W/ °C	Radiative conductance of the mount in a particular habitat	
U	m/s	Wind speed, measured at a height of about 10 m	
T_m	°C	Temperature of the mount	
T_b	°C	Body temperature	41 °C
T_a	°C	Ambient temperature, measured at a height of about 1.5 m above the ground	
T_{lc}	°C	Lower critical temperature, i.e. the ambient temperature below which the bird has to expend extra energy to maintain a constant T_b	
T_{uc}	°C	Upper critical temperature, i.e. the ambient temperature above which the bird has to expend extra energy to maintain a constant T_b	38-40 °C
T_{es}	°C	Standard operative temperature; by definition equal to T_a in the standard environment (the respirometry unit with $u = 1$ m/s)	
R_g	W/m ²	Global solar radiation	

4.1 Basal metabolic rate (BMR)

Animals always expend energy, even when they are inactive. Basal metabolic rate (BMR) is the energy expenditure of a non-productive, postabsorptive animal resting in thermoneutrality during the circadian rest phase (Aschoff & Pohl 1970). Estimates of BMR of Knot are provided by several independent studies (Kersten & Piersma 1987; Klaassen *et al.* 1990; Piersma *et al.* 1996; Kvist & Lindström 2001). BMR is estimated at 0.95 W, but is not an explicit parameter in our model. BMR is implicitly

present in estimates of energy expenditure that also include the costs of thermoregulation and activity.

Maximal rate of energy assimilation measured for Knots by Kvist & Lindström (2003) was 9.6 W, about 10.5 times BMR.

4.2 Maintenance metabolism (MMR) and daily existence energy (DEE)

From studies with heated taxidermic mounts of the Red Knot Wiersma & Piersma (1994) derive equations for the maintenance metabolism (MMR), defined as the basal metabolic rate (BMR) plus the extra costs for thermoregulation at environmental temperatures below the thermoneutral zone. They also show how these equations can be applied to other species of shorebirds.

Starting point are the Scholander curves describing heat loss of live birds in a standard environment:

$$\text{SMR} = K_{\text{es}}(T_{\text{b}} - T_{\text{a}}), \quad \text{when } T_{\text{a}} < T_{\text{lc}} \quad (5.1a)$$

$$\text{SMR} = \text{BMR}, \quad \text{when } T_{\text{lc}} < T_{\text{a}} < T_{\text{uc}} \quad (5.1b)$$

Next comes the equation describing the heat loss of the taxidermic mount in the field:

$$H_{\text{sm}} = (0.045 + K_{\text{u}} \cdot u^{0.75}) \cdot (T_{\text{m}} - T_{\text{a}}) - K_{\text{r}} \cdot R_{\text{g}} \quad (5.2)$$

To convert the heat loss of mounts into that of live Red Knots, heat loss values, H_{sm} were converted to standard operative temperatures, T_{es} , using the following equation:

$$T_{\text{es}} = 41 - H_{\text{sm}} / K_{\text{esm}} \quad (5.3)$$

The T_{es} calculated in this way can be substituted in equation (5.1) for T_{a} to obtain SMR.

The conductance at a given wind speed (K_{u}) and the radiative conductance (K_{r}) depend on the microhabitat: Table 4-2.

According to Wiersma & Piersma (1994), additional savings come from the shelter against the wind provided by feeding in a group (6%), whereas extra heat loss is incurred from not consistently facing the wind (2-9%).

Table 4-2: Estimates of conductance of a copper Knot in different microhabitats according to (Wiersma & Piersma 1994).

	K _u	K _r	Time budget Iceland & Wadden Sea	Time budget breeding grounds
Densely vegetated salt marsh	0.00294	0.00103		50%
Vegetated salt marsh	0.00478	0.00139	25% roosting	25%
Mudflat and bare salt marsh	0.00809	0.00080	75% (50% feeding + 25% roosting)	
On snow on tundra	0.00899	0.00197		
Behind tundra hillock	0.00707	0.00140		
On tundra hillock	0.01164	0.00107		25%
Dense group	0.00358	0.00052		
Open group	0.00455	0.00063		
Solitary	0.00614	0.00048		
Head in wind	0.00829	0.00067		
Flank in wind	0.00952	0.00062		

Originally, it was hoped to estimate MMR for all sites used by Knots from meteorological data and the equations provided by Wiersma & Piersma (1994). However, the above description shows that several complicated details are involved, requiring data (or assumptions) on microhabitat use and behaviour. Thus, estimating MMR for all sites used by Knots it is not a straightforward and simple exercise.

At present, the necessary work has been done for five different locations on the basis of meteorological data for each month of the year by Wiersma & Piersma (1994). The resulting estimates are listed in Table 4-3. The meteorological data on which these estimates are based are listed in Appendix 2 (Piersma 2002).

The monthly averages for the meteorological data for these five locations allowed us to investigate if they could be used to predict DEE of Knots in other locations. We followed (Piersma 2002), who estimates that DEE = 1.7 MMR. There was a very strong correlation of DEE with the average ambient temperature (Figure 4-1).

The resulting regression equation relating DEE (in kJ per day) to ambient temperature T_a (in °C) is:

$$DEE = 393.74 - 8.47T_a, N=60, R^2=0.88, P<0.001 \quad (5.4)$$

Thus, no less than 88% of the variation in the estimated DEE values is explained by variation in ambient temperature. The remaining variation is primarily due to variation in wind conditions. There is a remarkable difference between the Canadian tundra and the Siberian tundra.

Table 4-3: Monthly estimates of MMR of Red Knots in five different locations. For each location the source of the estimate is indicated.

Location	Banc d'Arguin, Mauritania	Wadden Sea	Iceland	Canadian tundra	Siberian tundra
Degrees	20N, 17W	53N,5E	65N,8E	80N,70W	75N,89E
Source	(Piersma 2002)	(Wiersma & Piersma 1994)	(Wiersma & Piersma 1994)	(Wiersma & Piersma 1994)	(Piersma 2002)
Month					
1	1.47	2.94	3.12	4.08	4.89
2	1.47	2.86	3.13	4.11	4.72
3	1.46	2.70	2.93	3.92	4.50
4	1.45	2.40	2.71	3.45	3.94
5	1.43	2.03	2.31	2.61	3.77
6	1.35	1.73	2.08	2.05	2.57
7	1.17	1.69	2.00	1.95	2.28
8	1.09	1.61	2.07	2.16	2.32
9	1.19	1.86	2.34	2.86	2.77
10	1.20	2.20	2.61	3.55	3.43
11	1.31	2.62	2.88	3.77	4.30
12	1.49	2.87	3.01	3.96	4.63

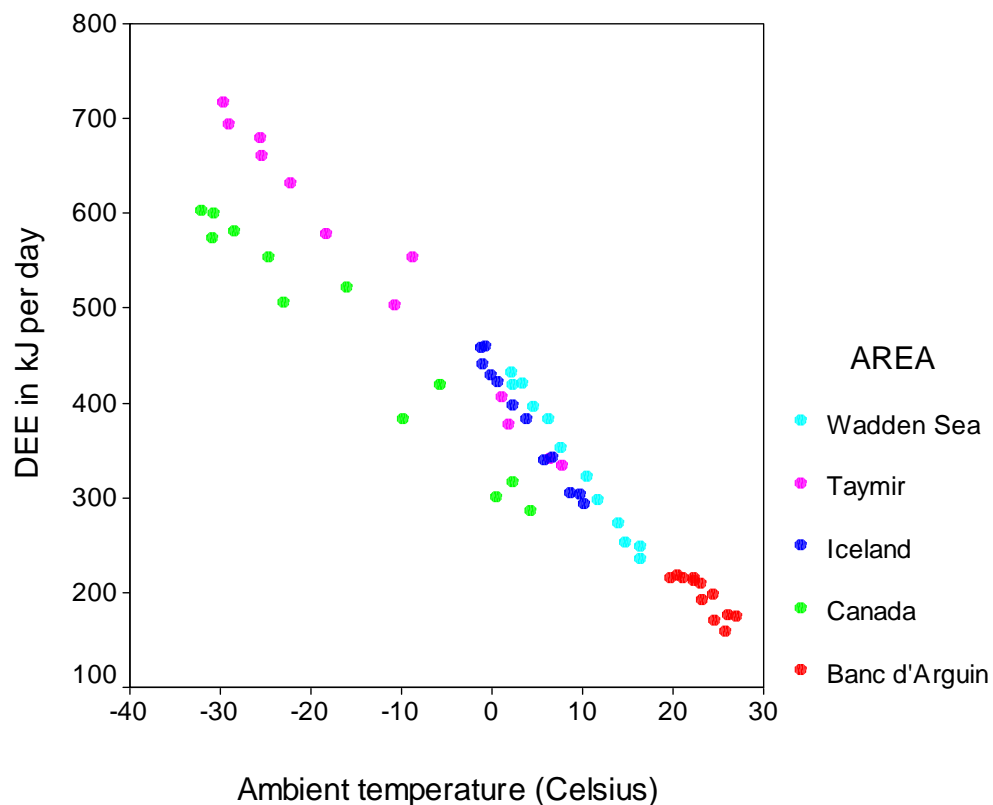


Figure 4-1: Predicted DEE (kJ per day) of Knot as a function of average ambient temperature (°C) per month for five locations. Based on data from Wiersma & Piersma (1994) and Piersma (2002).

For a same ambient temperature, DEE on the Canadian tundra is some 20% lower than DEE on the Siberian tundra. This is due to the Canadian tundra being much

less windy than the Siberian tundra. On Taimyr the average wind speed was 7.5 m/s, whereas this was only 2.5 m/s in Alert in Canada. Adding wind significantly increased the explained variance to 96%:

$$DEE = 248.54 - 9.95T_a + 23.49U, R^2=0.96, P<0.001 \quad (5.5)$$

Most of the remaining variance could be explained by radiation. When this variable was added to the equation, the explained variance increased to 99%:

$$DEE = 295.27 - 8.55T_a + 21.53U - 0.23R_g, R^2=0.99, P<0.001 \quad (5.6)$$

We found it easy to assemble temperature data for weather stations close to locations of interest and decided that the high correlation between DEE and ambient temperature made it unnecessary to invest a lot of effort in trying to collect wind and radiation data as well. Ambient temperatures were taken from the KNMI Climate Explorer (<http://climexp.knmi.nl>)¹ for weather stations close to the sites used by the Knots, which had more or less complete data for the years 1960-1990. These were averaged to yield the monthly mean temperature for each site (Figure 4-2).

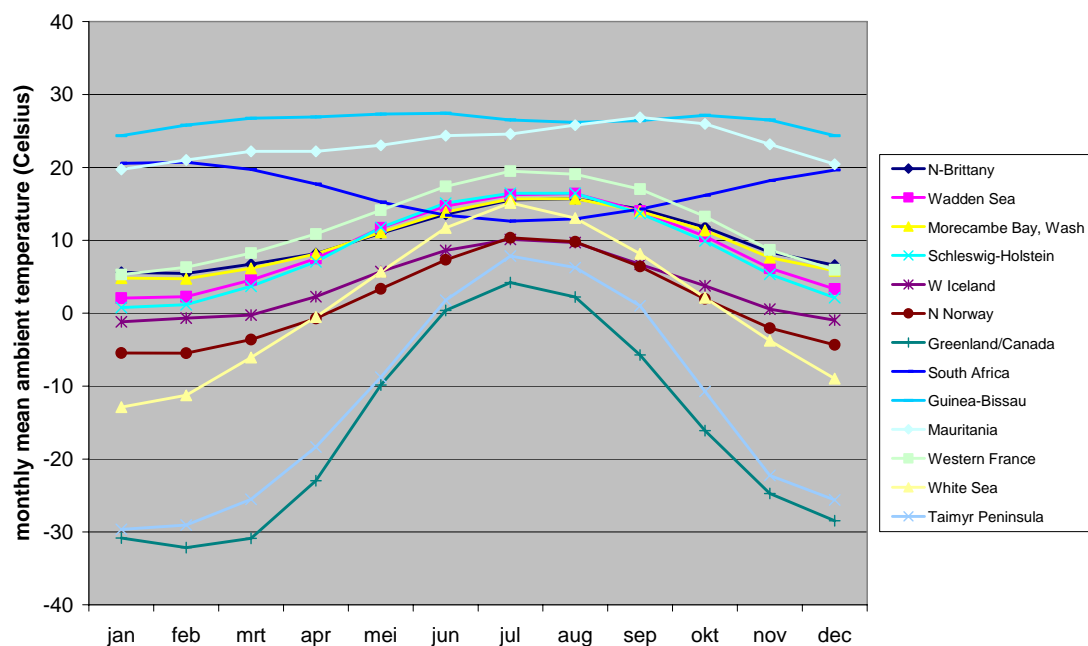


Figure 4-2: Monthly averages of ambient temperature (°C) for sites visited by Knots. Data were taken from the KNMI Climate Explorer and averaged for the years 1960-1990. Data are listed in Appendix 1.

Thus, we have an estimate of DEE for each site in every month for animals not changing weight. For some months we also have an estimate of the fuel deposition

¹ <http://climexp.knmi.nl> (the KNMI Climate Explorer developed by Geert Jan van Oldenborgh) was used to retrieve monthly mean temperatures from weather stations located near stopover sites. The temperature data set that was retrieved were adjusted values from the Global Historical Climatology Network – GHCN, indicated on the website as GHCN (adjusted).

rate (FDR); see chapter 3. We transformed both into units of x , describing the state of the animal (see chapter 2) and added them to obtain the DEE (in units of x) of animals gaining mass. We assumed that this was the best estimate of the maximum energy intake at that site and also assumed that at other times of the year it was unlikely that this maximum would be exceeded. Probably, this assumption overestimated maximum intake rates in other months, especially during winter when food availability is reduced. However, it allowed a calculation of maximum fuel deposition rates for months without empirical estimates for those months. We simply subtracted the DEE (in units of x) of birds not changing weight from the maximum estimate, as exemplified in Figure 4-3.

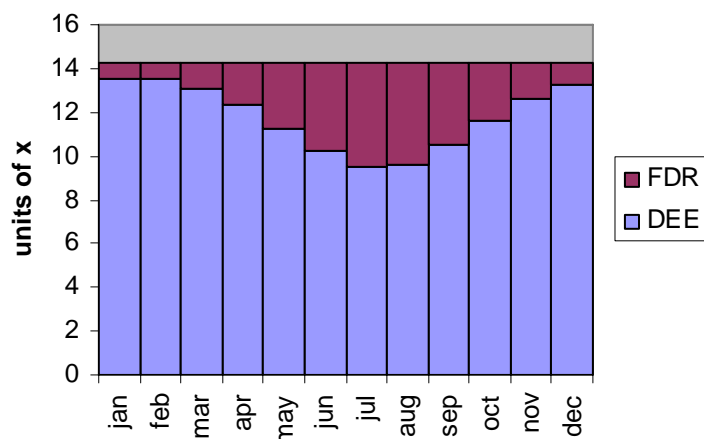


Figure 4-3. Construction of the maximum fuel deposition rate (FDR in units of x) for the staging site in Norway, where empirical estimates of FDR apply to May. DEE (in units of x) is estimated from meteorological data and applies to birds not changing mass.

4.3 Costs of fuelling, flight costs and flight range

The physiological ecology of flying, fasting and feeding in birds during migration was recently reviewed by McWilliams *et al.* (2004). They compare empirical estimates of flight costs in unrestrained birds during prolonged flight and compare these to predictions from aerodynamic theory. Empirical estimates were on average 13% lower compared to calculations with the model of Pennycuick (1989) and 28% higher compared to calculations with the same model but using a much lower body drag coefficient that was derived by Pennycuick *et al.* (1996). We will use empirical estimates wherever possible.

For Red Knots with a body mass exceeding 120 g the gross energy equivalent of reserve body tissue is estimated 35.0 kJ/g (Klaassen *et al.* 1990). The correlation on which this estimate is based has a squared correlation coefficient of 0.73. Since there will be errors in the measurements of the body mass changes and the metabolisable energy intake, it is better to use the reduced major axis to estimate the gross energy equivalent of the reserve body tissue (Ricker 1984). Dividing the estimate of 35.0 kJ/g by the correlation coefficient yields a value for the reduced major axis of 40.96.

Assuming that the body tissue consists exclusively of protein, fat and water, the composition of the reserve tissue can be estimated. For this estimation the energy density of fat is taken as 39 kJ/g and the energy density of protein is taken as 6 kJ/g by Klaassen *et al.* (1990), yielding an estimate that 81% of the reserve tissue consists of fat. This means that 32.77 kJ is contained in 1 g of body stores (31.65 kJ due to the fat and 1.13 kJ due to the protein).

Kvist *et al.* (2001) studied the flight costs of unrestrained Red Knots flying in a wind tunnel, including individuals carrying very high fuel loads. On the basis of their results, the flight range of a Knot flying in still air taking off with a body mass of 210 g and arriving with a body mass of 110 g has a flight range of 3420 km. The flight speed of migrating Knot is estimated at 60 km/h = 16.7 m/s (Piersma & van de Sant 1992). This means that a Knot flying all day in still air will cover 1440 km. The flight range parameter c in equation (2.7) of this report is estimated at 11677 km (equation (8) of Weber *et al.* (1998)).

5 Risk of predation

5.1 Introduction

Wherever they go, shorebirds are hunted by a variety of predators. In this chapter we first review the available evidence on the risk of predation, including circumstantial evidence and behaviours that can be interpreted as adaptive responses to the risk of predation. We then discuss how this risk should be incorporated in the model.

5.2 Empirical data on actual risk of predation

Table 5-1 lists information on studies that actually witnessed attacks of predators on shorebirds. Predators listed most often are Sparrowhawk, Peregrine and Merlin. Small shorebird species seem more at risk from predator attacks compared to large species.

Table 5-1: Summary of studies witnessing and measuring actual attacks of various predators on shorebird species.

Shorebird	Predator	Stage	Conclusion	Study
Redshank	Sparrowhawk	winter	Sparrowhawks preferentially attack vulnerable groups	(Cresswell & Quinn 2004)
Redshank	Sparrowhawk	winter	Attack decisions of Sparrowhawks depend primarily on vulnerability of Redshanks and not on abundance	(Quinn & Cresswell 2004)
Dunlin	Peregrine; Merlin; Northern Harrier	winter	94 Dunlins captured by Peregrine in 652 hunts; 62% attack flying flock (success 9.1%); 35% stealth on feeding or roosting flock (24% success); 4 Peregrines pirated Dunlins from Merlins; Closeness to shoreline vegetation is dangerous for Dunlin (peak in kill rate just after tide began to ebb); 7 of 13 kills by Merlin and all 5 kills by Northern Harrier in the shore zone	(Dekker 2003); (Dekker & Ydenberg 2004)
Redshank	Sparrowhawk	winter	Predation risk declines with distance from cover and with increasing flock size	(Whitfield 2003c)
Dunlin	Sparrowhawk	winter	Juvenile risk of predation positively related to Dunlin density	(Whitfield 2003a)
Redshank	Sparrowhawk	winter	31% juveniles and 6% adults predated; for both juv and ad predation mortality is. Risk of predation is density-dependent for both adults and juveniles	(Whitfield 2003b)
Dunlin	Peregrine, Merlin	winter	All 29 hunts of Merlin started as surprise attack (5 successful). Peregrines were more successful (33%) with surprise attack over saltmarsh (N=15) than with attacks in the open (9.3%, N=302)	(Dekker 1998)
Redshank	Sparrowhawk	winter	Lack of selection according to size or condition probably due to surprise attacks by Sparrowhawks	(Whitfield <i>et al.</i> 1999)
Dunlin, Least Sandpiper,	Merlin, American	winter	395 Dunlin (20.7% of population), 189 Least Sandpiper (11.9% of population), 26 Western	(Page & Whitacre 1975)

Shorebird	Predator	Stage	Conclusion	Study
Western Sandpiper, Sanderling	Kestrel, Marsh Hawk, Long-eared Owl, Short-eared Owl		Sandpiper (7.5% of wintering population), 18 Sanderling (13.5% of population) were taken by predators during the winter 1972-1973	
Oystercatcher, Ringed Plover, Grey Plover, Knot, Sanderling, Curlew Sandpiper, Dunlin, Bar-tailed Godwit, Redshank, Greenshank, Turnstone	Lanner Falcon, Peregrine, Barbary Falcon	autumn	Mainly Dunlin were taken (N=19 captures), although Knot and Bar-tailed Godwit were also very common. Most shorebirds present were adult, but the majority of killed shorebirds was juvenile. Juvenile Dunlin caught were in poor body condition to adults. Falcons hunted during high tide when low dunes provided cover for surprise attacks.	(Bijlsma 1990)
Redshank	Sparrowhawk	winter	Within a flock, redshanks that were figilant, close to the approaching rapoter, and close to their neighbours took flight earliest (as measured from videotape)	(Hilton <i>et al.</i> 1999a)
Oystercatcher, Ringed Plover, Grey Plover, Knot, Purple Sandpiper, Dunlin, Snipe, Bar-tailed Godwit, Curlew, Redshank, Greenshank, Turnstone	Sparrowhawk, Merlin, Peregrine	winter	Most attacks relied on surprise. On average 10% of attacks successful. For several shorebird species large part of overwinter mortality due to raptor predation. Minimum estimate percentage overwinter mortality due to raptors: Ringed Plover 2-6%, Grey Plover 2.5-7.9%, Knot 3.3-4.4%, Purple Sandpiper 0-12.5%, Dunlin 4.6-21.2%, Snipe 25-33.3%, Redshank 31.1-57.3%, Greenshank 0-13.3%, Turnstone 9.5-28.6% (Less than 1% for Curlew, Oystercatcher & Bar-tailed Godwit). Due to their kleptoparasitism, Carrion Crows increased shorebird mortality from predation	(Cresswell & Whitfield 1994; Cresswell 1996)
Redshank	Sparrowhawk	winter	Juvenile Redshank feed on saltmarsh, where intake rate is higher, but rate of predation is also higher (4.8 times) compared to mussel bed where adults feed	(Cresswell 1994a)
Ringed Plover, Grey Plover, Knot, Purple Sandpiper, Dunlin, Ruff, Redshank, Greenshank, Turnstone	Sparrowhawk	winter	Sparrowhawks preferentially killed prey with a body mass between 100-150 g. In total 214 Dunlin, 356 Redshank & 27 Turnstone killed	(Cresswell 1995)
Redshank	Sparrowhawk, Peregrine	winter	Flocking reduces the risk of predation but offers no substantial foraging gains	(Cresswell 1994b)

Meininger & Atta (1994) may be the only positive evidence that increasing fuel load increases the risk of being taken by avian predators (or being shot by human hunters): 5 Curlew Sandpipers shot by a hunter weighed 79.4 g, while 4 Curlew Sandpipers caught the previous night weighed 65.8 g. This difference bordered significance (t-test, $P=0.07$). When the comparison was made with all Curlew

Sandpipers caught in May the difference was highly significant (mean 67.3, $n=70$, t -test, $P<0.001$).

Apparent contrary evidence comes from Bijlsma (1990) who found that emaciated Dunlins were most often killed by falcons on the Banc d'Arguin. Similarly Dierschke (2003) found that migratory passerines killed on Helgoland by feral cats and Sparrowhawks were within the lightest 20% of the birds measured during ringing. However, light birds may have higher exposure due to more intense foraging and displacement to suboptimal habitats. The added risk of high fuel loads must be studied for animals that are otherwise in similar circumstances and behaving similarly - the mortality observed by Dierschke is a function of the intrinsic danger of the habitat, the actual escape performance of the bird once under attack and the anti-predator behaviour (Lank & Ydenberg 2003).

5.3 Circumstantial evidence of predation risk

There is circumstantial evidence that high wing loading negatively affects the risk of predation. There is a negative effect of wing loading (mass/wing area) on escape speed and escape angle for Least Sandpipers and Western Sandpipers (Burns & Ydenberg 2002). Zebrafinches loaded with extra mass have a 12% decreased velocity during takeoff (Nudds & Bryant 2002). Female great tits, the subordinate sex, lay on more fat during the day than males and take off at lower speed at dusk than at dawn (Krams 2002). Robins with a wing load of 0.19 g/cm² took off at a 39% lower angle than robins with a wing load of 0.13 g/cm² while velocity remained unaffected (Lind *et al.* 1999). From their experiments, Kullberg *et al.* (1996) calculated that blackcaps carrying 60% fat loads would have 32% lower angle of ascent and 17% lower velocity than blackcaps carrying no fat load. Increasing fuel load from 0 to 60% reduced flight velocity by 26% in sedge warblers, but there was no effect on angle of ascent in similar experiments by Kullberg *et al.* (2000).

There is also contrary evidence to the idea that wing loading has a negative effect on predation risk. A study of yellowhammers and greenfinches did not find support for a lowered escape performance at dusk, when weight was 7-8% higher. However, when alarmed, birds took off significantly faster and at a steeper angle than when not alarmed (Van der Veen & Lindstrom 2000). Similarly, Veasey *et al.* (1998) noted that the flight velocity of zebrafinches was lowered with increasing body mass, but that this relationship more or less disappeared when the flight speed of alarmed birds was studied. Willow tits studied by Kullberg (1998) were on average 7.7% heavier at dusk than at dawn, but there was no measurable difference, in average velocity, acceleration or angle of ascent, between dawn and dusk take-offs during attacks by a model predator. Similarly, Great Tits studied by Kullberg *et al.* (1998) were on average 7.9% heavier at dusk than at dawn, but there was no difference in flight velocity or angle of ascent, between dawn and dusk take-offs during attacks by a model predator.

5.4 Empirical evidence for adaptive changes in response to predation risk

There is evidence to suggest that shorebirds alter behaviour, morphology and life history traits in response to predation risk. The available evidence is listed in Table 5-2.

Table 5-2: Studies listing behaviour changes, or changes in morphology or life history in response to changes in predation risk that can be interpreted as adaptive changes.

Shorebird	Predator	Stage	Conclusion	Study
Redshank	Sparrow-hawk	winter	Redshank select risky feeding habitat (saltmarsh) when risk of starvation is high	(Yasue <i>et al.</i> 2003)
Western Sandpiper	Peregrine	migration	Migrating Western Sandpipers reduce length of stay (LOS) and body mass in response to increase of Peregrines	(Ydenberg <i>et al.</i> 2004)
Western Sandpiper, Semipalmated Sandpiper, Dunlin	Peregrine	migration	Truncation of parental care, timing of migration, moult, length of stay, use of stopover sites seem evolved to minimize risk from predation by migratory Peregrines	(Lank <i>et al.</i> 2003)
Golden Plover	Peregrine, Goshawk	winter	Peak in late autumn body mass has declined; probably in response to increased risk of predation	(Piersma <i>et al.</i> 2003a)
Western Sandpiper	Peregrine	migration	Sandpipers arriving with low body mass choose risky feeding site with high rate of food intake	(Ydenberg <i>et al.</i> 2002)
Dunlin	raptors		Over-sea flocking instead of roosting seems a reaction to high risk of surprise attacks by raptors	(Hötter 2000)
Redshank	Sparrow-hawk	winter	At low temperatures Redshank took more risk during foraging and Sparrowhawks were more successful. Redshanks took less risk on days when attack frequency by Sparrowhawks was high	(Hilton <i>et al.</i> 1999b)
Dunlin	Peregrine, Merlin		Over-sea flocking instead of roosting seems a reaction to high risk of surprise attacks by raptors	(Dekker 1998)
Redshank	Peregrine, Sparrowhawk, Merlin	winter	Sparrowhawks and Merlins have more success when Redshank crouch; Peregrines have more success when Redshanks fly. Redshanks adaptively vary escape behaviour with type of predator	(Cresswell 1993)
Dunlin	Merlin, Short-eared Owl	winter	Of 146 Merlin kills (single female), 73 were Dunlin. Juvenile Dunlin had higher risk of predation. Short-eared Owls also took more juvenile Dunlin (73%, N=18)	(Kus <i>et al.</i> 1984)

Several studies on birds other than shorebirds indicate that birds may lower their body mass in response to an increased risk of predation:

Blackbirds with high relative foraging rates have lowered body reserves during the winter (Cresswell 2003).

An experiment with Blue Tits showed that during long (but not short) days, the birds increased their reserves in response to interruption and reduced reserves in response to predation (Rands & Cuthill 2001).

Migrating blackcaps experimentally subjected to an increased perceived risk of predation from a stuffed predator during stopover, increased food intake and fuelling rate and attempted to depart earlier (Fransson & Weber 1997).

Great tits had higher body mass in periods and at locations where the risk of predation from Sparrowhawks was reduced (Gosler *et al.* 1995).

5.5 Modelling predation risk for arctic shorebirds

Dynamic modelling suggests that one form of predation risk (impaired ability to escape from an attacking predator) may be traded for another (more time spent foraging) (Brodin 2001).

(Weber *et al.* 1998) model predation risk as a function of both feeding intensity and fuel stores. In their notation, x represent the fuel stores, u the feeding intensity, i the site and g_i the gain. For the intensity-dependent predation risk, $\gamma(u)$, they assume the following relationship:

$$\gamma(u) = m_\gamma(i) u^b, \quad i < N \quad (5-1)$$

It is just one of many possible relationships that lead to an accelerating risk of predation when feeding intensity increases as long as $b > 1$. The term $m_\gamma(i)$ is a site-specific constant attack rate, such that predation risk per unit time does not exceed 1 for all foraging intensities.

They assume that carrying extra mass is also risky and that this risk is an accelerating function of the extra mass. They show that the mass-dependent predation risk, $\beta(x)$, can be approximated by the following equation for low predation rates for the particular form of the accelerating function that they assumed:

$$\beta_j(x) = m_\beta(i) \frac{(x + u g_j(i))^{a+1} - x^{a+1}}{(a+1) u g_j(i)}, \quad i < N \quad (5-2)$$

In this equation, a is a constant that is always greater than 1 and $m_\beta(i)$ is a site-specific constant, such that the predation risk per unit time does not exceed 1 for all possible masses.

They assume that the two predation risks are multiplicative in the following way:

$$m_j(x, u) = m_0(i) + \beta_j(x) \gamma(u), \quad i < N \quad (5-3)$$

In this equation, $m_0(i)$ is a site-specific constant background mortality risk. A justification for this equation, provided by (Houston *et al.* 1993), is that $\gamma(u)$ is the probability that a bird fails to detect an approaching predator and that $\beta(x)$ is the subsequent probability that the bird is killed in the ensuing attack.

For $m_0(1) = 0.001$, $m_v(i)m_p(i) = 0.000001$, $a = 2$, $b = 2$ and $g = 4$, the following graph (Figure 5-1) is obtained:

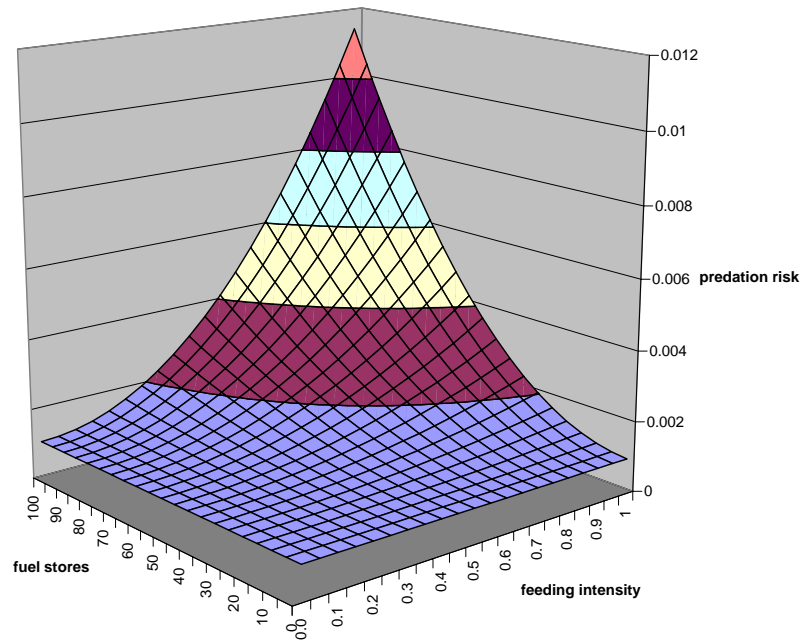


Figure 5-1: Predation risk (calculated according to equation 5-3) plotted against fuel stores and feeding intensity. High values for predation risk are only obtained when both fuel stores and feeding intensity are high.

The daily risk plotted in Figure 5-1 can be put into perspective by calculating the survival over six months if the birds ran this risk of predation during each day of the six month period:

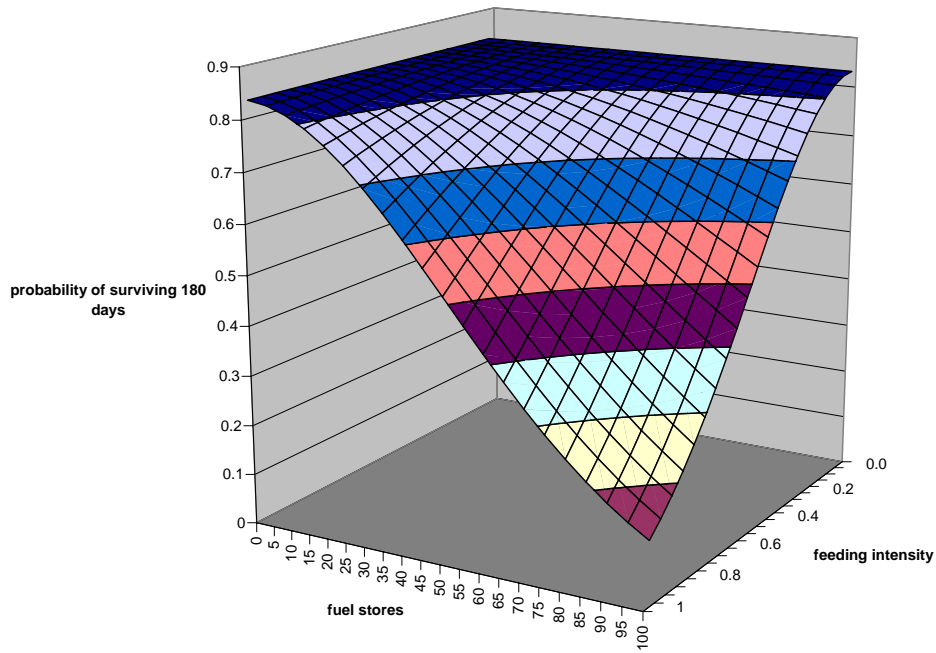


Figure 5-2: Probability of surviving 180 days, if the predation risk was each day similar to daily risk of predation plotted in Figure 5-1.

The higher predation rates lead to a six-monthly survival that is well below measured annual survival rates, which tend to exceed 70% in most cases (see later).

The major problem with the equation of Weber *et al.* (1998) is the assumption that the risks are multiplicative. The picture that emerges from reviewing the studies on risks of predation indicate that high rates of fuel gain can be obtained at the cost of a high risk of predation by feeding in more risky sites or at more risky times. The avian predators feeding on the shorebirds rely on surprise and the evidence that high mass carries high risks is at best equivocal. Thus, it seems better to have an equation that always leads to high risk with high feeding intensity, irrespective of the fuel stores. This is not possible when risks are modelled multiplicatively. The following, additive and equally ad-hoc, equation is therefore preferred:

$$m(x, u) = m_0(i) + m_\gamma(i)u^b + m_\beta(i)x^a, \quad i < N \quad (5-4)$$

For $m_0(1) = 0.0001$, $m_\gamma(i) = 0.01$, $m_\beta(i) = 0.005$, $a = 4$ and $b = 4$, this leads to the following graph (Figure 5-3) for predation risk as a function of fuel stores and feeding intensity.

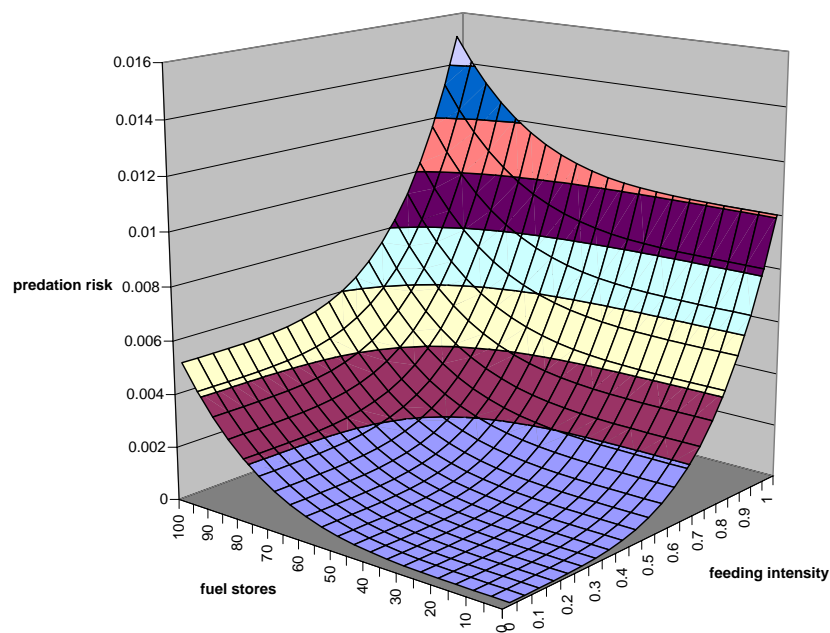


Figure 5-3: Predation risk (calculated according equation 5-4) plotted against fuel stores and feeding intensity. High values for predation risk can be obtained when either fuel stores or feeding intensity are high

The probability of surviving a period of 6 months at this daily risk is represented in the following graph (Figure 5-4):

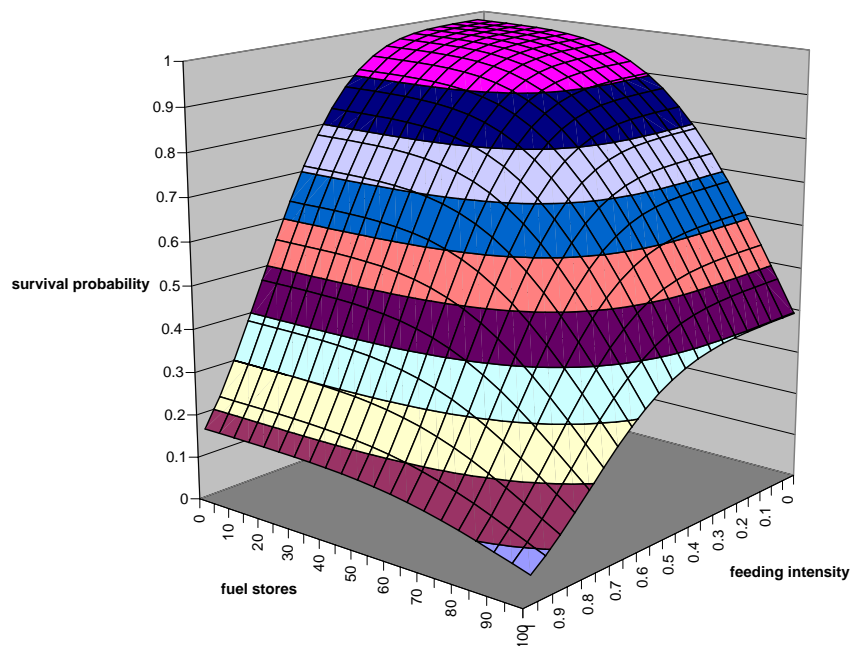


Figure 5-4: Probability of surviving 180 days, if the predation risk was each day similar to daily risk of predation plotted in Figure 5-3.

6 Reproductive success (terminal reward)

6.1 Introduction

Stochastic Dynamic Programming models of migration (like DYNAMIG) revolve around the function that describes how a bird's fitness depends on the date that it arrives at the breeding site and the state (nutrient store level) that it arrives in. In the backward simulations, this *terminal reward function* provides the basis for formulating the optimal behavioural decision for each time/state combination. In the forward simulations, it determines the actual fitness result of the optimal migration strategy given the environmental conditions encountered underway.

As a proxy for fitness we use in our model the reproductive success over the (remaining) lifetime of the individual (parameter in the model: F). F is the sum of reproductive success in the current breeding season and that in future breeding seasons, both of which depend on the adult surviving the current breeding season. To achieve reproductive success in the current season (parameter in the dynamic model: R), the bird has to make it to the breeding site and survive until the end of the breeding season (model parameter S), lay eggs, hatch them and raise the chicks to fledging. If the bird survives the current season, it receives a fixed future reproductive success (model parameter: B_0), that is determined by the average annual survival and the average reproductive success:

$$F = S (R + B_0) \quad (6.1)$$

The relationship between arrival time and arrival state on the one hand and survival S and reproductive success R are thus a crucial part of the SDP model. This relationship has been extensively studied in several arctic-breeding geese, e.g. (Ebbinge 1989; Prop & Black 1998; Prop *et al.* 2003). For another major group of arctic migratory birds, shorebirds or waders, it has been far less well explored, but shorebirds differ from geese in several potentially important aspects. While geese are large herbivorous birds that arrive on the breeding grounds with significant nutrient stores that are used to at least partly produce the clutch of eggs, and sometimes also to sustain metabolism during incubation, the much smaller mainly insectivorous shorebirds produce eggs mainly from nutrients assembled after arrival on the breeding grounds (Klaassen *et al.* 2001; Morrison & Hobson 2004). This implies that in geese arrival state may affect reproductive success directly via clutch size, while in shorebirds (which show a rather invariant clutch size) effects are more likely to be indirect and expressed through time (laying date). Nevertheless, also in shorebirds nutrient stores may serve to buffer starvation risk arising shortly after arrival, while they may also be used to transform the body from a 'flying' state to a 'breeding' state (Morrison *et al.* 2005).

In this chapter we derive functions describing R and S in relation to arrival date and arrival state, mainly based on results of fieldwork carried out at Medusa Bay, NW

Taimyr, Siberian arctic, in 2000-2002 (Tulp & Schekkerman 2001; Tulp *et al.* 2000; Schekkerman *et al.* 2004). A direct approach, in which we attempted to catch and colour-mark birds upon arrival and follow them through the breeding season to determine breeding success, failed because of difficulties with capturing birds, few marked individuals settling to breed in the study area, high predation levels and the difficulty of estimating fledgling production in nidifugous birds. Therefore, we also adopted an indirect approach, in which we studied food availability, climatic conditions, and growth and energy expenditure of birds to identify potential energetic bottlenecks and selective forces on the timing of breeding. One such force is the growth and survival of chicks, that was shown to depend on the availability of surface-active arthropods as food, which in turn is affected by both date and weather conditions. A second important period in the breeding cycle is directly after arrival, when the adults face a relatively high risk of starvation caused by snow cover or freezing temperatures. Apart from the Medusa Bay studies, we also use results from earlier studies conducted in Northern Taimyr (Schekkerman *et al.* 2003) and from the literature (reviewed by Meltofte *et al.* (2006)).

Our field studies were done on several other shorebird species, and results for different aspects of the reproductive process stem from different species, depending on which was most amenable to study that aspect. However, in this report we parameterise the SDP model for Red Knots *Calidris canutus* only, as for this species the best parameter estimates are available for the migratory journey. In this chapter we construct the terminal reward function for that species. Arctic-breeding Calidrinid sandpipers seem sufficiently similar in size and general breeding ecology for the results to be applicable to most species as far as the general shape of the terminal reward function is concerned.

We describe S and R for two locations: the Taimyr Peninsula as a representative of the Siberian Arctic, and NE Greenland as a representative of the Nearctic. For Greenland, we use the same data and rules as for Taimyr, except that different snow and weather data are used (from Zackenberg Station in NE Greenland, Zackenberg Ecological Research Operations reports).

For Taimyr, predictions are made for arrival dates running from 1 June to 31 July (31 August). Snow and temperature data for May, which would allow predictions for earlier arrival dates, are lacking at the moment. It seems probable that terminal reward rapidly declines for arrival dates earlier than 1 June, especially for birds in a less than average condition: May is usually still cold in Taimyr and snow cover is often almost complete. In Greenland, spring arrives earlier than in Taimyr and weather and snow data for May were available; therefore predictions have been made for arrival dates running from 1 May.

This terminal reward model is set up in the form of Excel-worksheets. It has no built-in stochasticity, but many of the parameter estimates are based on data that would allow this.

6.2 Knots breeding on Taimyr

6.2.1 Current Reproductive Success

The probability of successful reproduction in the current year is modelled as the product of an arriving bird surviving the breeding season S and the reproductive success R that a surviving individual will enjoy: $R \cdot S$. While survival is modelled as a function of both arrival date and arrival mass ($S_{x,t}$), reproductive success (of a surviving individual) is dependent only on arrival date (R_t). R_t is the product of nest survival and chick survival. If the clutch is lost, there is a (date-dependent) possibility that a replacement clutch is laid. The reproductive output of the second clutch is the product of the probability that a replacement clutch is laid, nest survival and chick survival. All these components are described as a function of arrival date. We thus assumed that clutch and chick survival were independent of arrival condition, and ignored the (likely) possibility that arrival condition affects the time between arrival and laying.

6.2.1.1 Adult survival upon arrival $S(x,t)$

In order to reproduce successfully, a bird must survive the breeding season. Upon arrival, shorebirds face the possibility that they starve when snow and ice conditions make feeding impossible for a time that exceeds the capacity of the birds' nutrient stores. To quantify the probability that this occurs, we estimated the survival time under starving conditions given the bird's fuel stores upon arrival (in days), and calculated the probability that starving conditions prevail for this long after each possible arrival date. We assume that there is no other source of mortality on the breeding grounds besides starvation risk.

For energy expenditure of Red Knots under starvation conditions and body mass at death, we used estimates of 200 kJ/day and 100 g respectively, derived from *islandica* Knots that starved to death during winter cold spells in the Dutch Delta and Wadden Sea (Piersma *et al.* 1994). 200 kJ/d is the estimate of maintenance metabolism (including thermoregulation costs but excluding activity) based on weather data for five days prior to death and equations provided by Wiersma & Piersma (1994) for vegetated saltmarsh. From these data we calculate the time needed to starve from arrival mass to death as follows (Table 6.1)

Table 6-1: Calculation of the time to starvation for a given arrival mass for Red Knot.

Arrival mass (g)	Fuel stores (x) ¹	Mass at death (g)	Fat stores ² (g)	Protein reserve ² (g)	Energy metabolised at death ³ (kJ)	DEE while starving (kJ/d)	Starvation Time (d)
110	0	100	0	10	70	200	0.4
120	10	100	0	20	140	200	0.7
130	20	100	10	20	530	200	2.7
140	30	100	20	20	920	200	4.6
150	40	100	30	20	1310	200	6.6
160	50	100	40	20	1700	200	8.5
170	60	100	50	20	2090	200	10.5
190	80	100	70	20	2870	200	14.4
210	100	100	90	20	3650	200	18.3

¹ Unit used in the SDP model; ² Assumption: at body mass <120 g all stores consist of protein, and above 120g of fat. ³ Energy yield of fat 39 kJ/g, of protein 7 kJ/g.

Thus, we effectively assume that Knots starving on the tundra during cold weather after arrival do so inactive and somewhat sheltered. This assumption is supported by the observation of Davidson & Morrison (1992) that Red Knots strongly reduce activity under cold conditions in the first week after arrival in N Ellesmere Island, Canada.

Starvation conditions were considered to apply when the daily average temperature did not exceed -2°C. On those days, maximum temperature probably did not rise much above 0°C and the tundra surface likely stayed frozen, preventing the birds to probe for buried larvae. The likelihood that such conditions prevail for at least the estimated survival time was calculated from daily average temperatures measured in NW Taimyr (Dikson) in June-August over the 30 years 1973-1992. Logistic regression equations were fitted to the resulting survival probabilities to smooth them over arrival date t and state x:

$S_{x,t} = \exp(\text{logit } A) / (1 + \exp(\text{logit } A))$, where

$\text{logit } A = -49.4 + 0.2506t + 0.0873M_a$

$\text{logit } A = -32.06 + 0.2506t + 0.0873x$

with t= time in days since January 31st, and M_a =arrival mass (g), which is equivalent to

in the SDP notation with x= fuel stores (= $M_a - 110$ g) (6.2)

Het resultaat is afgebeeld in Figuur 6-1.

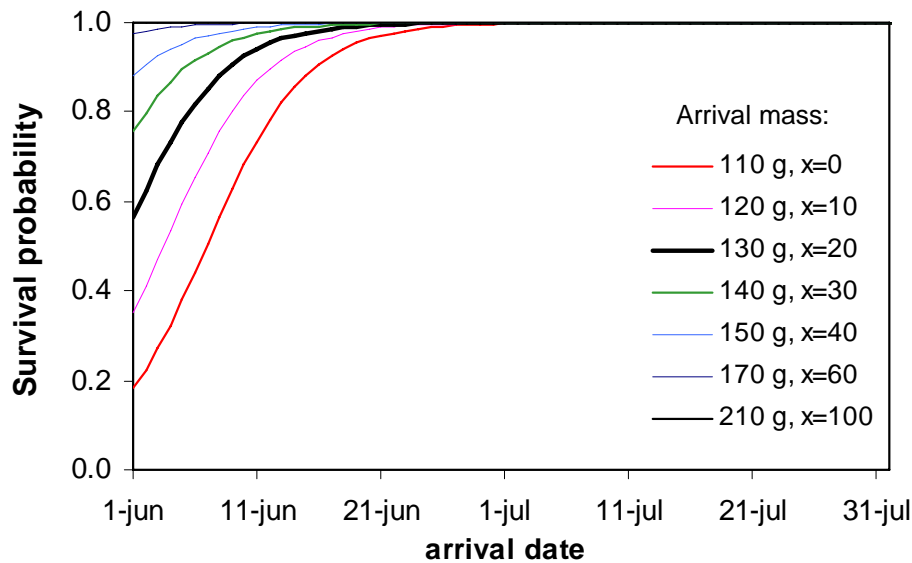


Figure 6-1: The probability of adult survival over the breeding season in relation to arrival date and arrival mass for Taimyr Knots. The average mass of Red Knots arriving in NW Taimyr was 130 ± 8 g ($N=5$, (Schekkerman *et al.* 2004)).

6.2.1.2 Length of the pre-laying period

Upon arrival on the breeding grounds, arctic shorebirds need time for transformation of body organs and to assemble nutrients for egg formation. Not much is known about this period, although it is clear that feeding (weather and snow) conditions in the arrival period affect its length. It is also likely that arrival condition may have an effect, as birds arriving with larger stores may need less time to collect the nutrients for a clutch. Since only the earliest shorebird eggs show isotopic traces of imported nutrients (Morrison & Hobson 2004), this is probably not a direct mechanism, but arrival stores may be used for self-maintenance or rapid rebuilding of digestive and other organs after the migratory flight (Morrison *et al.* 2005), and thus save time compared to a situation where that has to be done from locally assembled food processed by these same, still atrophied organs.

Nevertheless, we have ignored a possible effect of arrival mass on the length of the prelaying period, mainly because we don't know its magnitude. Based on an egg mass of 19 g (Simmons *et al.* 1983), and an estimated yolk mass of 7 g (Sotherland & Rahn 1987), the energy content of a four-egg Red Knot clutch can be estimated at 567 kJ. If this energy is accumulated over 7 days, the daily metabolisable energy intake MEI can be estimated at $567/7 + DEE$, with $DEE=360$ kJ/d (Piersma *et al.* 2003b), so at 385 kJ/d fat stores yield 39 kJ/g, so 10 g roughly equate to 1 day's MEI. This is likely to be an overestimate because stores are unlikely to consist of fat only and energetic efficiency of egg production will be less than 1. This very crude preliminary estimate suggests that each 10 g of fuel stores would save about 1 day on the pre-laying

period. Given the range in reported arrival masses (c. 120-150g) this would mean a difference of 1-2 days in laying dates, which would have only a small effect on R.

For Siberian Knots we estimated the time between arrival and start of laying at 7 days. At Cape Sterlegov, N Taimyr in 1994, 50% of the maximum number of Knots observed during daily transect counts in the arrival period was reached on 15 June, while the mean first-egg date was 22 June (Tulp *et al.* 1998). While Morrison *et al.* (2005), report that in N Ellesmere Island, Canada, *islandica* Knots arrive around 1 June (“late May- 3 June”) and mean first egg dates occur 15 days later (but SD=7d), we used the Taimyr estimate of 7 days in our calculations. Egg-laying was assumed to take 4 days from the laying of the first egg.

6.2.1.3 Nest survival

Egg-laying can only start as soon as suitable patches become snow-free. In addition, early in the season when snow-free patches are scarce, predation rates can be higher than later on (Byrkjedal 1980). As long as there is (partial) snow cover, predators only need to search the snow-free areas to find nests. Nest survival was therefore modelled as a function of snow cover. In the model we used the average snow cover (Medusa Bay 2000-02) during a 25-day period following the first-egg date (4 d laying + 21 d incubation) starting 7 days after the arrival date. We assume a baseline predation probability of 50% in snow-free conditions, a value which is derived from observed predation rates in Taimyr in three years (Schekkerman *et al.* 2004) (but this input parameter can be changed in the spreadsheets). Furthermore we assume that predation pressure increases from this baseline value in proportion with the fraction tundra surface covered by snow; i.e. that predation pressure doubles when 50% is snow-covered, and increases tenfold when only 10% is snow-free. The probability H_t that the nest survives to hatching given arrival date t was thus calculated as:

$$H_t = H_b \cdot (1 - FS_t) \quad (6.3)$$

with H_b = baseline hatching probability (default 0.5), and FS_t = fraction snow cover

Figure 6-2 shows that snow cover has only a limited effect on clutch survival, and this effect is even partly compensated by a high probability that early-lost clutches are replaced (see below). Because they are present later in the season, survival of replacement clutches (see below) is practically unaffected by snow.

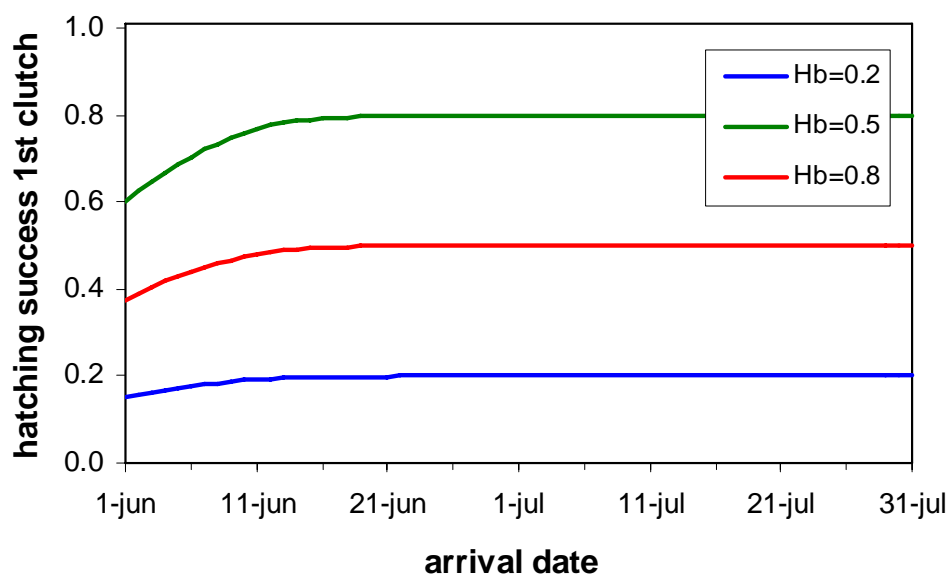


Figure 6-2: The probability of nest survival in relation to arrival date, for three different levels of baseline nest survival H_b

6.2.1.4 Probability and survival of a replacement clutch

When a clutch is lost (e.g. due to predation), shorebirds may produce a replacement if the breeding season has not progressed too far. The extent to and the latest date at which this happens may vary between species. We based the probability that a lost clutch is replaced on observations in Dunlin *Calidris alpina* at Medusa Bay in 2000-02 (especially 2000, when predation was high). Because a large proportion of the local Dunlin population was colour-ringed, replacement clutches of individual birds could be registered. Only clutches predated before the end of June were replaced in this species (Tulp *et al.* 2000).

We assumed that all predation events take place at 40% of the incubation period, which approximates the average predation day given an exponential decline of the number of nests surviving. For Red Knots this is on day 9, 20 days after the arrival date (7 pre-laying, 4 laying, 9 incubation). The logistic regression equation relating replacement probability V_t to arrival date t is:

$$\text{logit } V_t = 58.7 - 0.507(t+20), \quad \text{with } \text{logit } V_t = \ln(V_t/(1-V_t)) \quad (6.4)$$

The resulting relationship is depicted in Figure 6-3. In the calculation of $V(t)$, the production of a replacement is made conditional on the failure of the first clutch, by multiplying with $(1-H_t)$, where H_t =hatching probability of the first clutch.

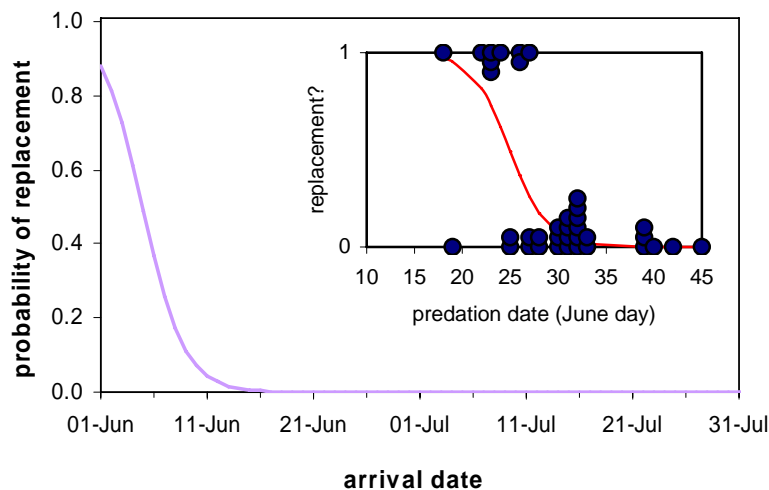


Figure 6-3: The probability that a lost clutch (lost on average 20 days after arrival) will be replaced. The inset shows the actual data on which this line is based, i.e. the relationship between replacement probability and predation date of Dunlin nests at Medusa Bay (Tulp *et al.* 2000).

For Red Knots in which probably no more than a few hundred nests have been found worldwide, replacement probability is unknown, although Simmons *et al.* (1983) state “no replacements”. As a largish sandpiper breeding at extreme latitudes, there might indeed hardly ever be time for a Knot to successfully fledge chicks from a replacement clutch, but very early nest losses may still be replaced. The slightly longer pre-laying and incubation periods of Red Knot than of Dunlin shift the replacement curve two days to the left and hence reduces V ; only Knots that arrive early have an opportunity to produce a replacement clutch, and replacements contribute only marginally to R in the Taimyr Knot model.

Survival of replacement clutches was modelled in the same way as for first clutches, but now using average snow cover over a period starting at 25 days after the arrival date (7 d pre-laying, 4 d laying, 9 d incubation until predation of the 1st clutch, and 5 d relaying interval). The length of the relaying interval was estimated from observations in Dunlin, as no data is available for Red Knots. In practice, this means that replacement clutches are largely ‘free’ of the intensified predation that early clutches suffer, because snow cover has declined strongly when they are produced.

6.2.1.5 Chick survival: first clutch

Arctic-breeding shorebirds have precocial chicks that feed for themselves on surface-active invertebrates from the day of hatching onwards. Work on several species has shown a strong correlation between growth rate of chicks and surface-activity of arthropods: Curlew Sandpiper, Red Knot, Dunlin and Little Stint. In Little Stint and Curlew Sandpiper, indications were found that these growth rate effects translate into survival (Schekkerman *et al.* 1998; Schekkerman *et al.* 2003; Schekkerman *et al.* 2004).

On Taimyr, activity of surface-dwelling invertebrates (the main food of shorebird chicks) was measured by pitfall trapping, and showed a very high weather-dependence superimposed on a unimodal seasonal pattern (Schekkerman *et al.* 2003; Tulp & Schekkerman 2005). Low temperature, rainfall, and strong winds drastically reduce arthropod activity. The amplitude of short-term weather-induced effects was at least as large as that of the seasonal pattern. Based on data from Medusa Bay in 2000-02, we constructed regression models and used these to 'postdict' arthropod availability over the 30-year period from temperature records obtained at nearby Dikson (Tulp & Schekkerman 2005) (Figure 6-4a-b).

Red Knot chicks were shown to be able to grow normally only when arthropod biomass caught in 20 pitfall traps exceeded 100 mg per day (Figure 6-4c)(Schekkerman *et al.* 2003). Therefore, we assumed that Red Knot chicks fledge successfully when the average food arthropod activity exceeds 100 mg/20traps/day over the entire 18 day fledging period, which starts 33 days after the arrival date (7 days pre-laying, 4 days egg laying, 22 days incubation). We used the most recent 20 years of arthropod predictions (1983-2002) because the 30-year data series showed an increasing trend in mean temperature (Tulp & Schekkerman 2005).

Survival of chicks from replacement clutches was modelled in the same way as for first clutches, but now over a fledging period starting at 59 days after the arrival date (7d pre-laying, 4d laying, 9d incubation until predation of the 1st clutch, 5d relaying interval, 4d laying and 22d incubation of second clutch). The length of the relaying interval was estimated from observations in Dunlin, as no data is available for Red Knots.

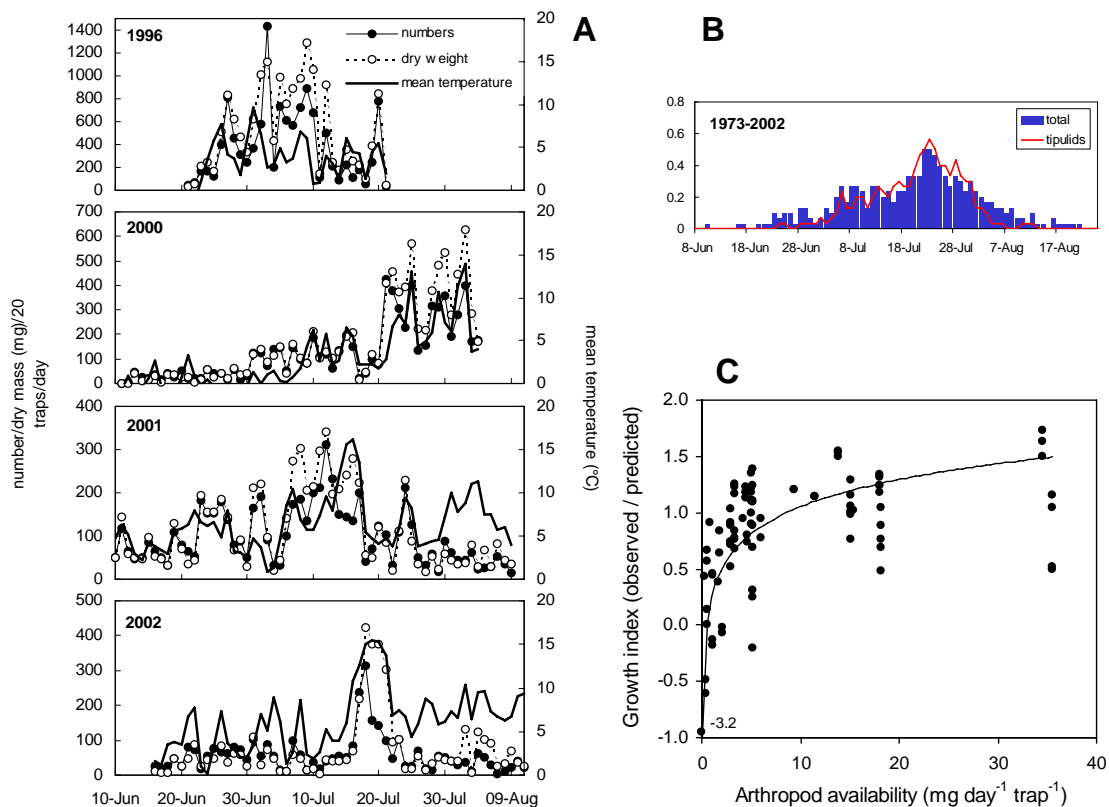


Figure 6-4. Empirical data underlying the modelling of chick survival against date. A: Seasonal change in numbers and dry mass of arthropods and mean temperature in the four study years at Medusa Bay. In all years arthropod activity was closely correlated with temperature, but this broke down after mid-July (see 2001-2002), indicating that there is also a significant effect of date; from Tulp & Schekkerman (2005). B: These effects were strong enough to allow 'postdiction' of arthropod abundance based on historical temperature data; the figure shows the probability that total dry mass or that of Tipulidae (an attractive prey type for chicks) exceeded 5 mg/trap/day for each date, calculated over the years 1973-2002). C: The threshold value of 5 mg/trap/day was based on the observation that the growth rate of Red Knot chicks declines sharply when arthropod abundance falls below this level (growth rate was expressed as an index: observed growth over a recapture interval, divided by the average growth expected for chicks of this size); from Schekkerman et al. (2003).

Figure 6-5 shows how simulated chick survival depends on arrival date in our model. We also calculated probabilities for other arthropod availability criteria (average >50g, ≥ 9 days out of 18 >100mg, or >50mg) which yielded different levels of chick survival but rather similar end-dates of the period suitable for growth (Figure 6-5). Conditions for survival of first-clutch chicks do not vary much as long as arrival dates fall between 1 and 20 June. With later arrival dates, chick survival decreases and arriving after the end of June means that the chance that chicks find enough food to grow and fledge seems negligible. To be able to fledge chicks from a replacement clutch, birds should arrive earlier, preferably not much later than 10 June. However, arriving before 1 June also results in a reduced breeding success, as chicks will hatch before the food peak in most years (not shown in Figure 6-5, but start of decline for early dates just visible).

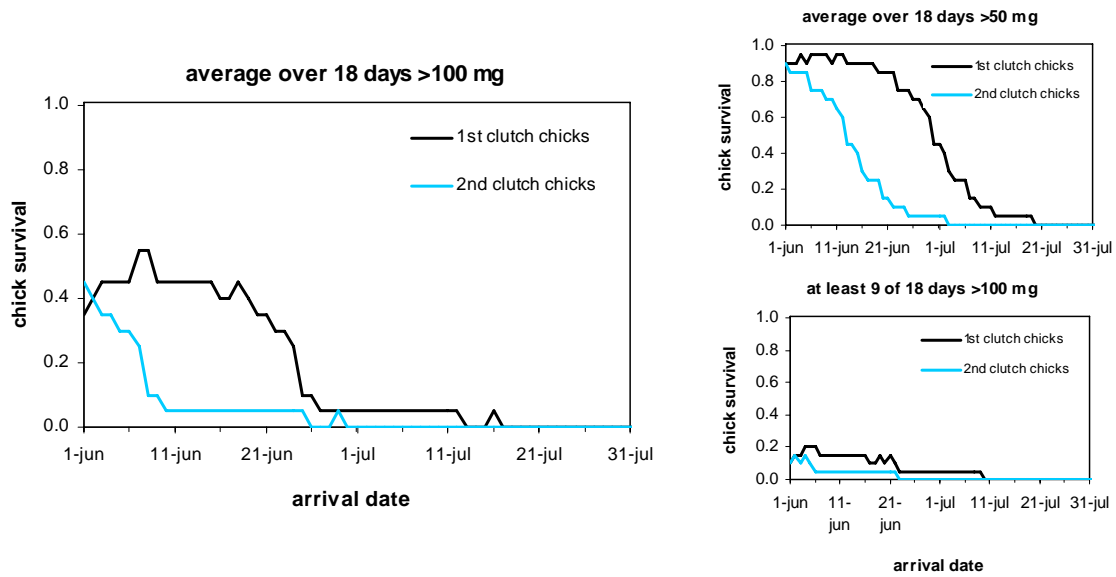


Figure 6-5: The predicted probability of survival for chicks from first and second clutches in relation to arrival date. The left panel shows the model used; the right panels show alternatives with different criteria for arthropod availability needed for chicks to survive (panel titles; average arthropod biomass in 20 traps over 18 days >50 mg, or biomass >100 mg on at least 9 out of a row of 18 days).

6.2.1.6 Reproductive success

Reproductive success (CRS) in the current season is the product of the probability of surviving that season ($S_{x,t}$), and the probability R_t that a surviving bird fledges chicks:

$CRS = S_{x,t} * R_t$, where

$$R_t = H_t * C1_t + (1 - H_t) * H_t * V_t * C2_t \quad (6.5)$$

with

H_t = hatching probability of the clutch (both 1st and 2nd)

V_t = probability that a lost 1st clutch is replaced

$C1_t$ = probability of a chick from a first clutch fledging

$C2_t$ = probability of a chick from a replacement clutch fledging

In words, CRS is conditional on the survival of the adult after arrival on the breeding grounds ($S_{x,t}$), and then made up of the sum of the contributions of first clutches and replacement clutches to breeding success (R_t), each of which is the product of hatching success and chick survival. Replacements are only produced if the first clutch fails, and with a date-dependent probability. We assume that first and replacement clutches are subject to the same baseline hatching probability H_b . Figure 6-6 shows how the different parameters together shape CRS, for the mean observed arrival mass of 130g.

Through the effect of adult survival, reproduction in the current year depends not only on arrival date but also on arrival mass (Figure 6-7). While birds that arrive with large fuel stores would do best by arriving in early June, birds arriving with low stores run a high risk of starvation at this time and would best arrive in mid-June, but they will suffer a reduction in breeding output anyway.

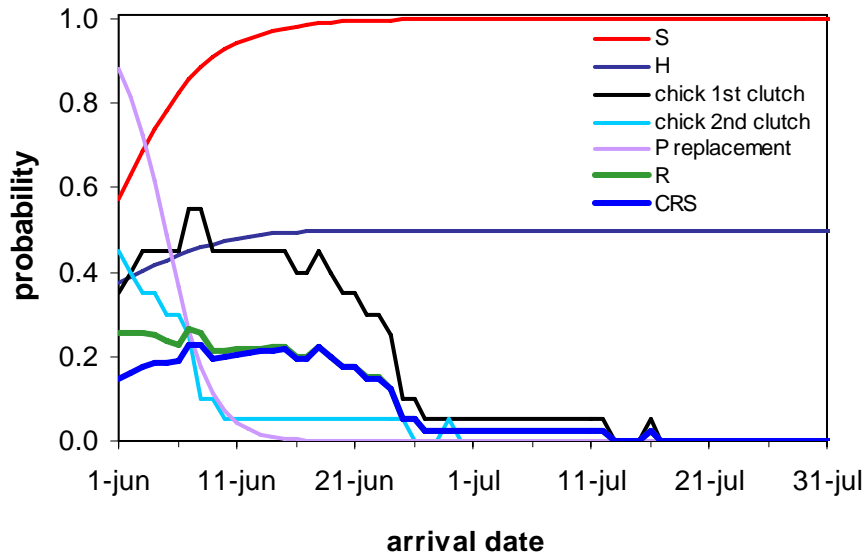


Figure 6-6: Current reproductive success (CRS) of Red Knots on Taimyr, as the product of several constituent probabilities as described in the text, for the mean observed arrival mass of 130g. S = adult survival, H = clutch survival, chick = chick survival, $P_{\text{replacement}}$ = probability of laying a replacement clutch, R = probability of raising one or more chicks to fledging for a bird that survives, $CRS = S \cdot R$.

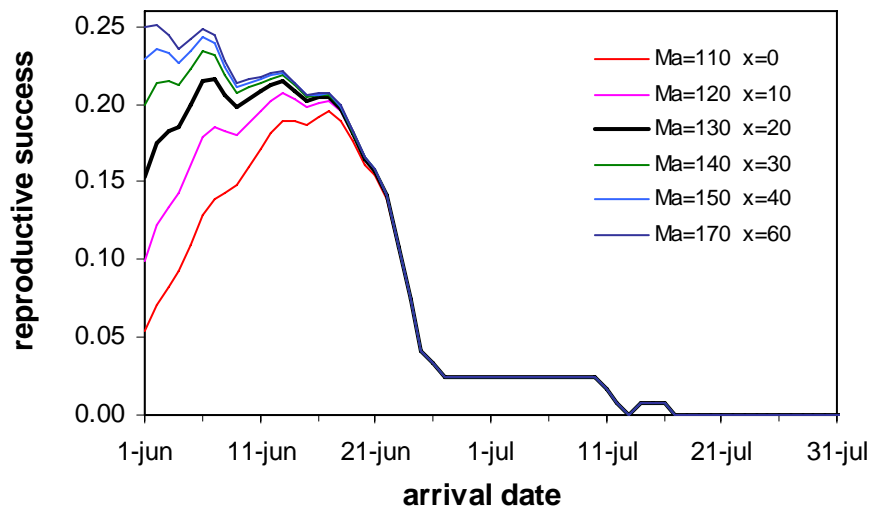


Figure 6-7: Current reproductive success (CRS, 3-day running mean of probability of fledging chicks) for Taimyr Knots as a function of arrival date and arrival mass (M_a) / arrival stores (x). The effect of arrival mass arises through adult survival.

6.2.2 Future Reproductive Success and Fitness

To calculate expected future reproductive success (FRS), we multiplied the (arrival date-dependent) probability of surviving the current breeding season S_t with the expected future reproductive success of a bird that does survive this season (B_0). B_0 is the number of future breeding seasons based on a constant annual survival rate S_a , multiplied by the expected reproductive output during those seasons. The latter can take many different values, depending on assumptions about the birds' behaviour in future years. One possibility is that even if a bird arrives late in the current year and therefore suffers reduced breeding success, if it survives it will do better in the following years and reap the maximum breeding success in those years. This will cause overestimation because the birds are likely to 'do something wrong' or suffer bad luck in at least some of the future years. On the other hand, assuming that they will arrive at the same date and mass in the future as in the current year is even less plausible (it implies that birds cannot learn and that conditions along the migration route are the same every year), and would lead to an underestimate of fitness. We (arbitrarily) used an intermediate approach and estimated reproductive success in future seasons as the mean expected R over the range of body masses (120-140 g) and arrival dates (6-20 June) observed in the field²³:

$FRS_{d,m} = \sum_{y=1..15} S_{x,t} * B_0$, in which

$$B_0 = S_a^y * R_{mean} \quad (6.6)$$

For Red Knots, we used a mean annual survival rate of 0.8 ((Boyd & Piersma 2001), *C.c. islandica*) and a maximum reproductive life span of 15 years (at $S_a=0.8$ only 3% is still alive at age $y=15$). With the current default values of the model, $R_{mean}=0.2$.

Lifetime reproductive success or expected fitness (F), which constitutes the terminal reward in the SDP models, is simply the sum of current and future reproductive success:

$$F_{x,t} = CRS_{x,t} + FRS_{x,t} \quad (6.7)$$

In the current formulation F is a sum of probabilities. If F were to be used in a population dynamic setting (e.g. a population model), it could be multiplied by the average clutch size (4) to get the number of young fledged.

In long-lived species like Red Knot, FRS makes up a large proportion of F (Figure 6-8, but note that FRS will be somewhat overestimated). This means that a Knot would not suffer a major reduction in expected fitness by skipping a breeding season, as long as it makes sure that it survives to breed later. Also apparent in Figure 6-8 is the very small contribution of replacement clutches to LRS. Our uncertainty about

² This may still result in some overestimation as breeding seasons may be skipped altogether

³ Morrison *et al.* (2005) report a higher mean (140-145 g) and a wider range (125-170 g) for *islandica* Knots arriving at Alert, N. Ellesmere Island; we preferred to use Taimyr observations, even if only few.

the occurrence of replacements in Red Knots therefore is of no consequence for the model results.

In the present formulation, the reduction in expected fitness suffered by birds arriving early with low body masses (Figure 6-9) is caused only by reduced survival in the current year.

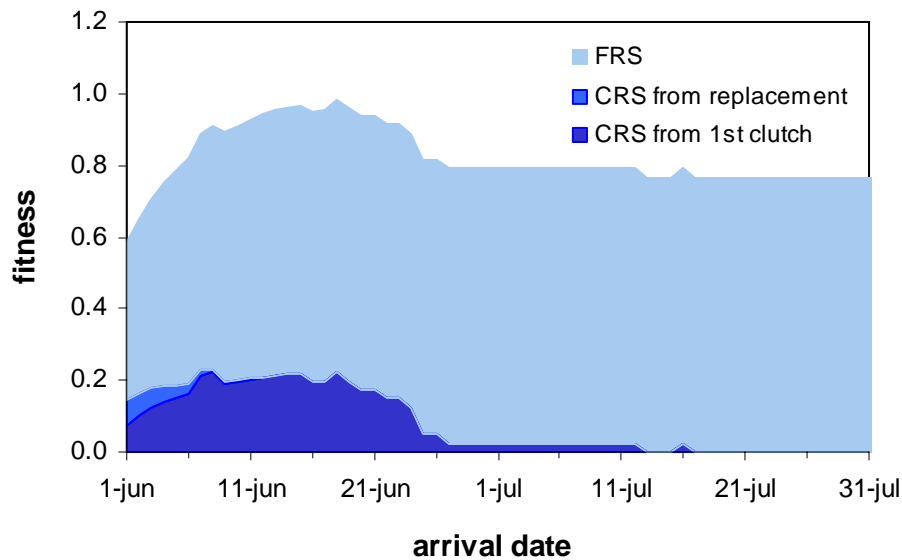


Figure 6-8: Expected fitness (lifetime reproductive success) of Red Knots in Taimyr subdivided by reproductive success from the first and second clutch in the current season and future reproductive success, for the mean arrival mass, 130 g (3 day running averages).

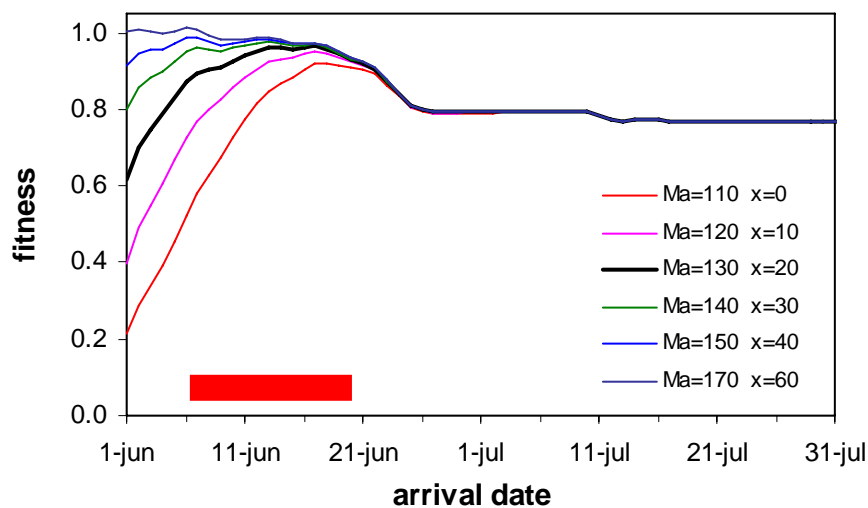


Figure 6-9: Expected fitness (lifetime reproductive success) of Red Knots in Taimyr, dependent on arrival mass (3 day running averages). The red bar denotes observed arrival dates in Taimyr (see text).

It is interesting to compare predicted arrival dates of Red Knots to actual observations from Taimyr. At Cape Sterlegov in 1994, Knots were already present when the expedition arrived on 11 June. Numbers counted along daily transects increased until 17 June, but migrating flocks were seen until 19 June. At Medusa Bay in 2001, daily migration watches revealed the first Knot on 8 June, with peak migration around 10 June, and passage ending around 17 June. In 2002 as many as 50 Knots were already present at our arrival on 8 June. These flocks were gone after 13 June (Schekkerman et al. 2004, and unpublished data). These data suggest that most Knots probably arrive in Taimyr between 7 and 17 June, with few arriving before 5 or after 20 June, which agrees well with expectations derived from Figure 6-9.

6.2.3 Smoothed terminal reward

In the previous paragraphs, survival and reproductive success were modelled on a daily basis, based on measured field data. The shape of the relationship with arrival date was not constrained to a simple mathematical form and the resulting graphs show irregularities that are not easy, and also not relevant, to include in the terminal reward function in the larger dynamic programming model. To obtain a smooth terminal reward function that can be incorporated in the model, we fitted a Gaussian curve to the expected numbers of chicks that an adult that survived the current breeding season would fledge. To calculate the expected number of chicks fledged, we used the following equation:

$$ERS_t = (H1_t * C1_t + (1-H1_t) * H2_t * R_t * C2_t) * L, \quad (6.8)$$

Where:

$H1_t$ = hatching probability of the 1st clutch

$H2_t$ = hatching probability of the 2nd clutch

R_t = probability that a lost 1st clutch is replaced

$C1_t$ = probability of a chick from a first clutch fledging

$C2_t$ = probability of a chick from a replacement clutch fledging

L = clutch size (set to 4 eggs)

The Gaussian curve relates ERS to date (t in days since January the 31st) as follows:

$$ERS = A * \exp(-(t-B)^2 / C^2) \quad (6.9)$$

Nonlinear regression yielded the following estimates for the parameters (Table 6-2):

Table 6-2: Parameter estimates of the Gaussian curve relating expected fledgling production to arrival date of Red Knots in Taimyr, subject to the condition that arriving adults survived to reproduce.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% Confidence Interval	
			Lower	Upper
A	1.1078	0.0190	0.980	1.055
B	127.94	0.6692	126.61	129.27
C	18.0255	0.8132	16.41	19.64

The estimates for each arrival date and the fitted Gaussian are depicted in Figure 6-10.

To obtain the fitness expectation (in terms of chicks fledged) for the current season, we multiply ERS with the probability of survival upon arrival at a given date with a given fuel load $S_{t,m}$ (Figure 6-11). The dependence of $S_{t,m}$ on arrival date (t) and mass (M_a) is given in equation 6.2. To this we must add the expected number of chicks fledged in the future, which is estimated at 0.75 times 4 = 3 for adults that survive upon arrival (Figure 6-12).

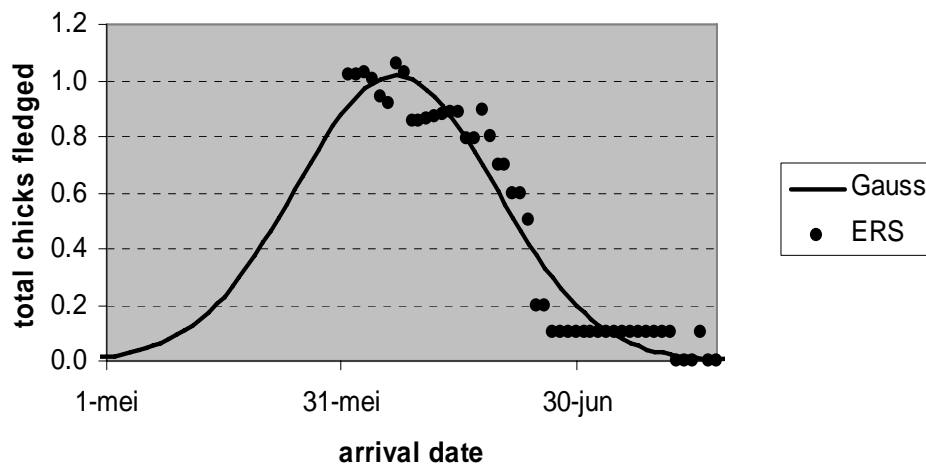


Figure 6-10: Expected number of chicks fledged by Red Knots on Taimyr as a function of arrival date for surviving adults. The line indicates the Gaussian curve fitted to the estimated data points. The parameters for this curve are in Table 6-2.

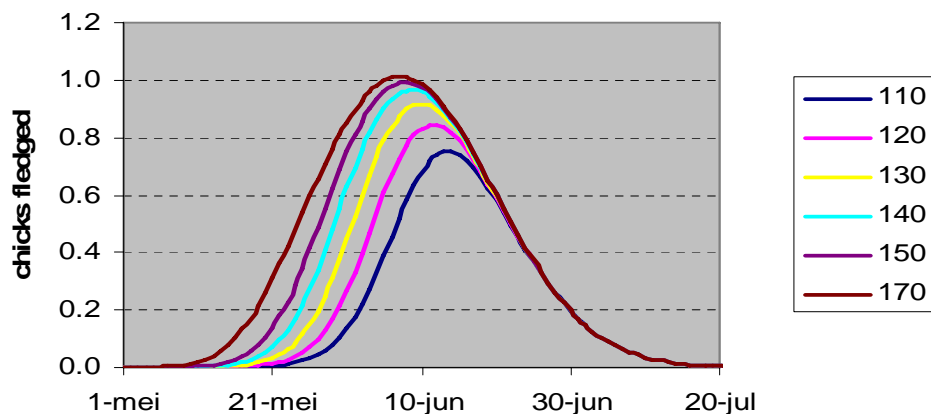


Figure 6-11: Expected number of chicks fledged by Red Knots on Taimyr as a function of arrival date, including the effect of arrival date on survival of adults arriving with different body masses (different lines).

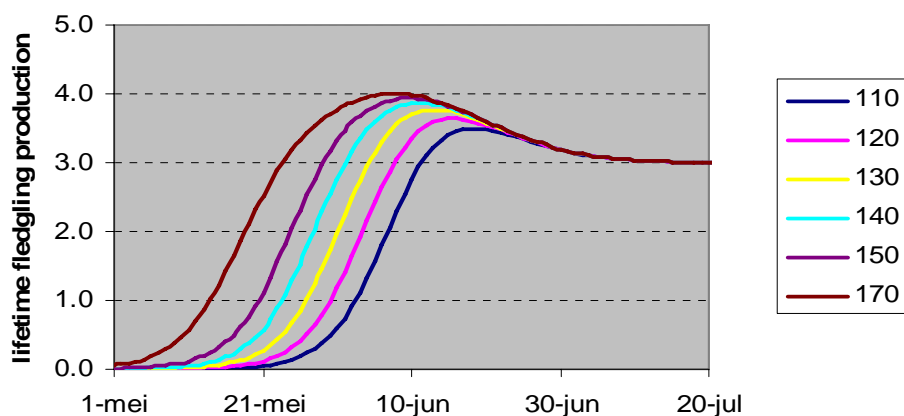


Figure 6-12: Expected number of chicks fledged over the life span of Red Knots in Taimyr as a function of arrival date, including the effect of arrival date on survival of adults arriving with different body masses in the current breeding season (different lines).

6.3 Knots breeding on Greenland

There are clear differences in the weather between Taimyr and Greenland, and good weather data were available for Greenland. Below, we use these data to arrive at a terminal reward function for Greenland. However, for some parameters of the reproduction model we lack field data for Greenland, and were thus forced to assume that specific details that we measured in Taimyr also apply to Greenland. In the following paragraphs, only those points are highlighted in which the Greenland model differs from the Taimyr model.

6.3.1 Current reproductive success

6.3.1.1 Adult survival upon arrival

We assume that Table 6-1 also applies to *islandica* Knots confronted with a frozen tundra upon arrival. Thus for Greenland Knots we inserted in equation 6.2:

$\text{logit } A = -43.41 + 0.2461d + 0.0652M_a$ if M_a = arrival mass (g), and

$\text{logit } A = -28.61 + 0.2461t + 0.0652x$ if the SDP notation is used (t =time in days since January the 31st and x = fuel stores).

Because temperatures start rising and snow disappears earlier in the spring in NE Greenland than in NW Taimyr, Knots can arrive about one week earlier without negative effects on survival probability (Figure 6-13).

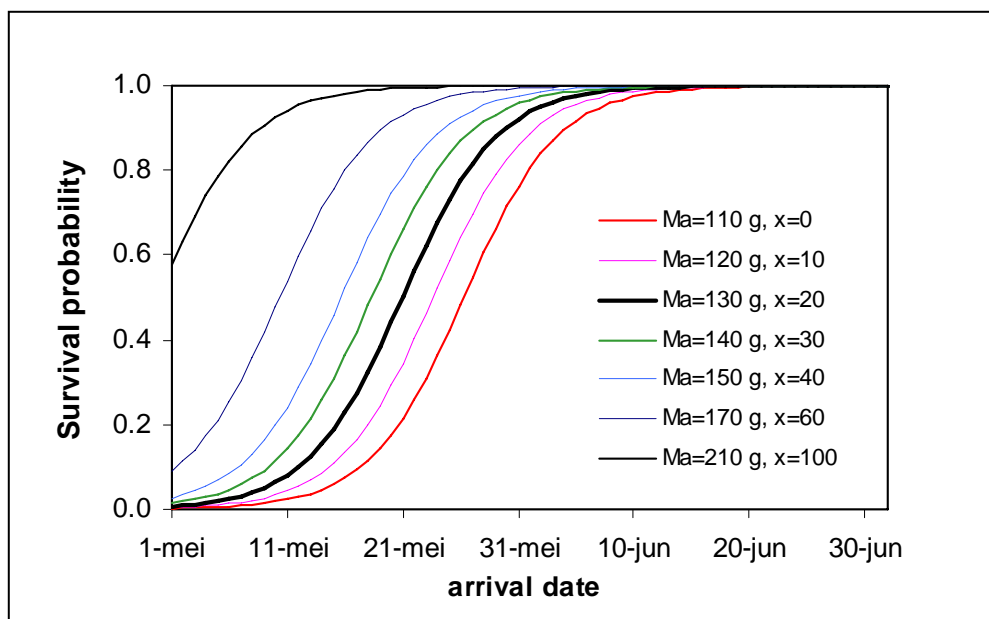


Figure 6-13: The probability of adult survival over the breeding season in relation to arrival date and arrival mass for Greenland Knots. The average mass of Red Knots arriving in NW Taimyr was 130 ± 8 g ($N=5$, (Schekkerman et al. 2004)).

6.3.1.2 Chick survival & reproductive success

In modelling hatching success and chick survival for Red Knots breeding in Greenland, we assumed that everything is the same compared to Taimyr, except for the weather. Thus we used the same equations as for the Taimyr Knots, but based all calculations on weather data obtained in Greenland, at Zackenberg in 1996-2002. This shorter period (7 years instead of 20) may mean that the annual variability in weather conditions is less well captured in the Greenland data. We used the Greenland weather data to predict insect availability and the probability that chicks find sufficient food to grow and survive, but also here used the equations derived for Taimyr. Because fewer years of weather data were available the lines for chick survival in Figure 6-14 are less fluent than those for Taimyr Knots, but this does not affect the general shape of the curves. The timing of the modelled peak in food availability that determines chick survival is similar to that in Taimyr, but because the summer weather is generally better in Greenland than in Taimyr, modelled maximum values of chick survival are higher here, and even reach 1 which will not be reached in reality. To improve future versions of the model, daily arthropod abundance data should be collected and analysed to derive equations specific for this site.

The lines of overall reproductive success in Figure 6-14 and Figure 6-15 show a peculiar bimodal shape, which is the result of the interplay between the effects of snow cover on hatching success and the probability of replacement clutches. Possibly because the Zackenberg study area spans a much greater altitude range than the Taimyr site, more snow persists for longer and this depresses modelled hatching rates. Knots that arrive between 5 and 10 June still face this depressed hatching rate

but increasingly fail to produce a replacement clutch (in the model; the date-dependence of replacement probability was assumed to be the same as in Taimyr but empirical data are lacking). Birds arriving after 10 June can no longer replace a lost clutch, but fewer of their clutches are lost because snow has largely disappeared by then. In reality, the relationship with date is probably more unimodal.

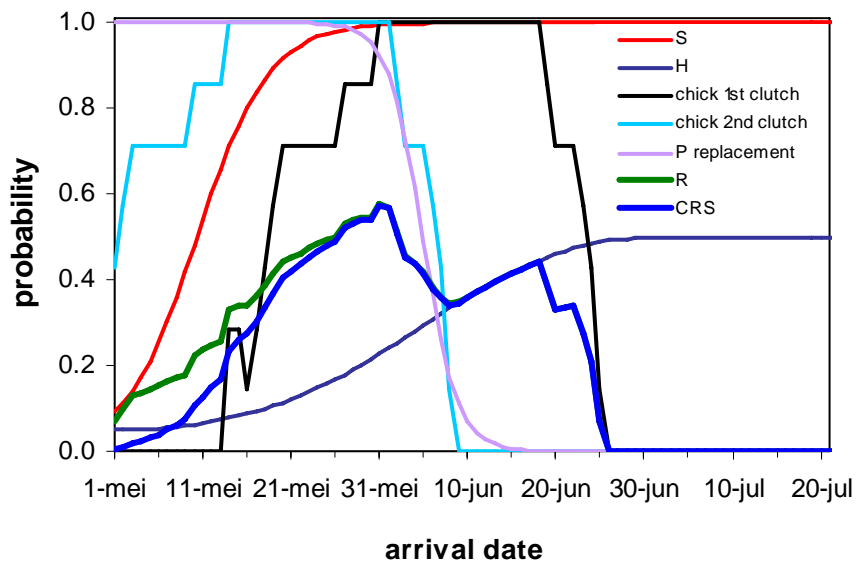


Figure 6-14: Current reproductive success (CRS) of Red Knots in Greenland, as the product of several constituent probabilities as described in the text, for the mean arrival mass of 130g. S = adult survival, H = clutch survival, chick = chick survival, $P_{\text{replacement}}$ = probability of laying a replacement clutch, R = probability of raising one or more chicks to fledging for a bird that survives, $\text{CRS} = S \cdot R$.

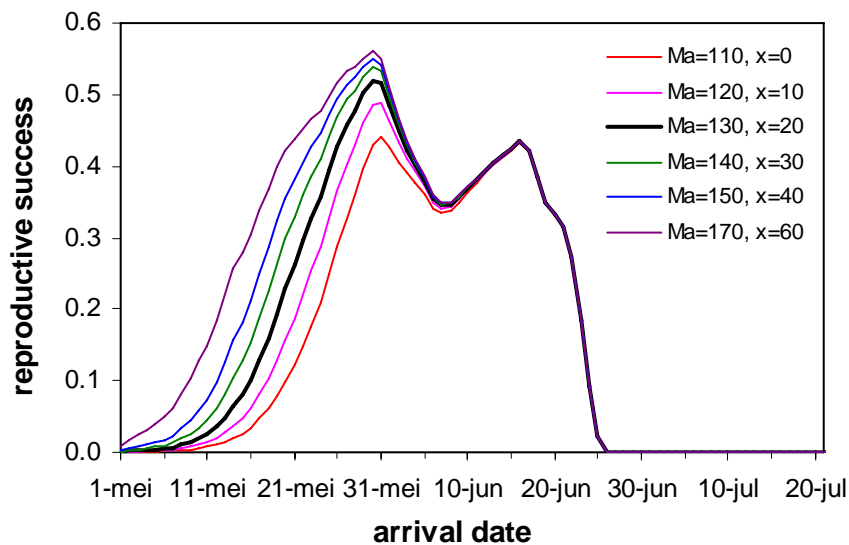


Figure 6-15: Current reproductive success (CRS, 3-day running mean of probability of fledging chicks) for Greenland Knots as a function of arrival date and arrival mass (M_a) / arrival stores (x). The effect of arrival mass arises through adult survival.

6.3.2 Future and lifetime reproductive success

Future and lifetime reproductive success for Greenland Knots were modelled in the same way as for Taimyr Knots. Because Knots can arrive about a week earlier in Greenland than in Taimyr without a higher risk of starvation, but the modelled timing of the insect peak is similar, the ‘window’ of arrival dates for which successful reproduction is possible is wider in the Greenland model than in Taimyr (Figure 6-16 and Figure 6-17).

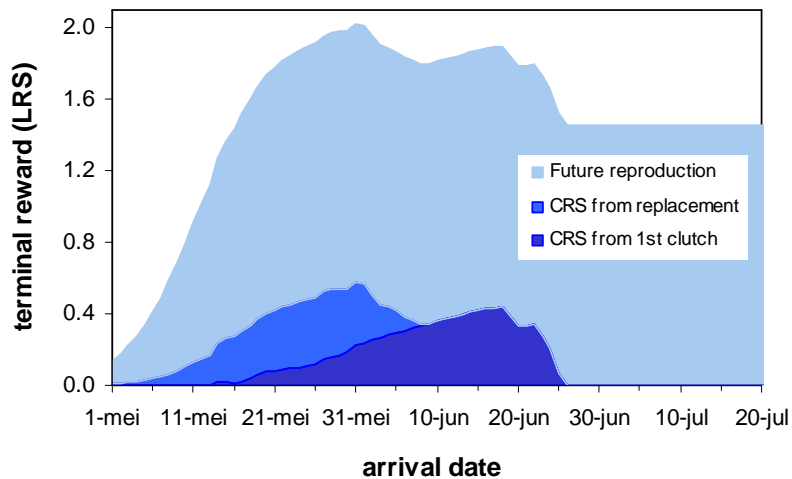


Figure 6-16: Expected fitness (lifetime reproductive success) of Red Knots in Greenland, subdivided by reproductive success from the first and second clutch in the current season and future reproductive success, for the mean arrival mass, 130 g (3 day running averages).

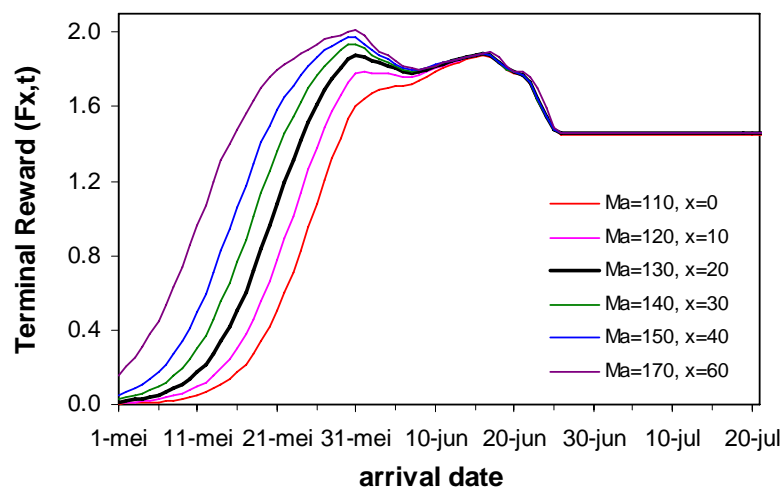


Figure 6-17: Expected fitness (lifetime reproductive success) of Red Knots in Greenland, dependent on arrival mass (3-day running averages).

6.3.3 Smoothed terminal reward

If the modelled terminal reward is smoothed by fitting a Gaussian curve to it (Table 6-3), the bimodality is smoothed out which probably better reflects the real shape of the relationship (Figure 6-18).

To obtain the fitness expectation (in terms of chicks fledged) for the current season, we multiply ERS with the probability of survival upon arrival at a given date with a given fuel load $S_{t,m}$ (Figure 6-19). The dependence of $S_{t,m}$ on arrival date (t) and mass (M_a) is given in equation 6.2. To this we must add the expected number of chicks fledged in the future, which is estimated at 0.75 times 4 = 3 for adults that survive upon arrival (Figure 6-20).

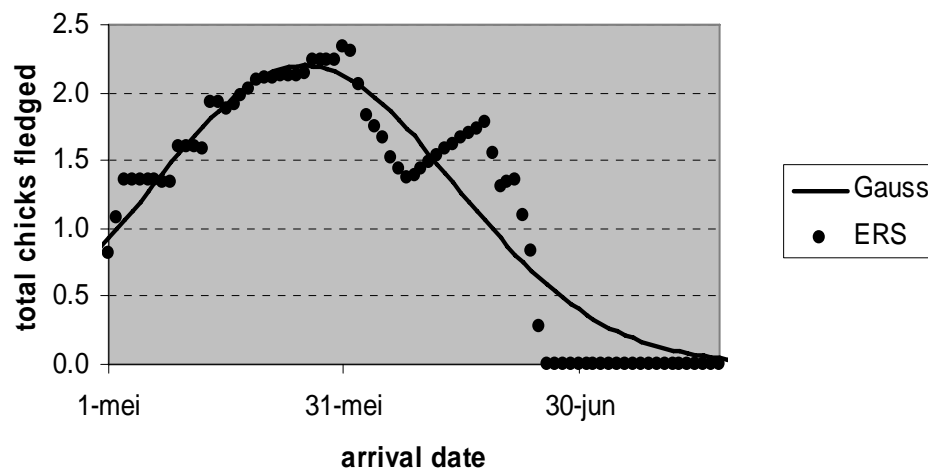


Figure 6-18: Expected number of chicks fledged by Red Knots in Greenland as a function of arrival date for surviving adults. The line indicates the Gaussian curve fitted to the estimated data points. The parameters for this curve are in Table 6-3.

Table 6-3: Parameter estimates of the Gaussian curve relating expected fledgling production to arrival date of Red Knots in Greenland, subject to the condition that arriving adults survived to reproduce.

Parameter	Estimate	Asymptotic SE	Asymptotic 95% Confidence Interval	
			Lower	Upper
A	2.2021	0.0475	2.108	2.296
B	115.96	0.522	114.93	116.99
C	26.928	0.824	25.296	28.56

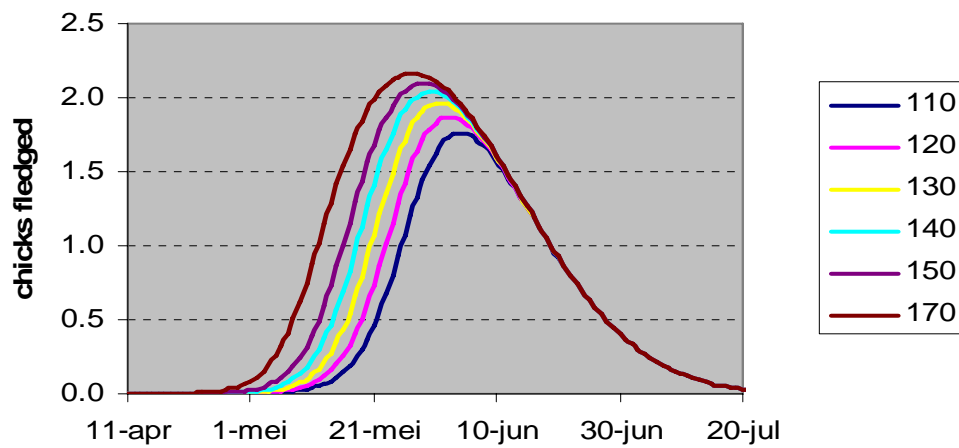


Figure 6-19: Expected number of chicks fledged by Red Knots in Greenland as a function of arrival date, including the effect of arrival date on survival of adults arriving with different body masses (different lines).

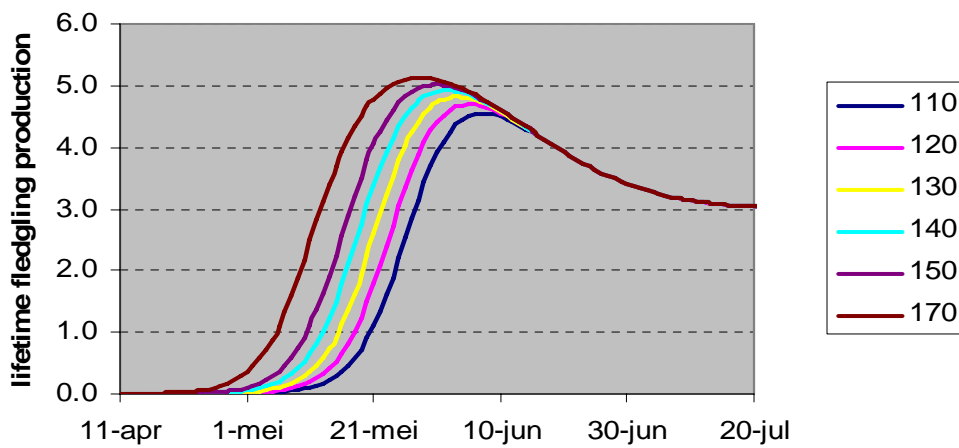


Figure 6-20: Expected number of chicks fledged over the life span of Red Knots in Greenland as a function of arrival date, including the effect of arrival date on survival of adults arriving with different body masses in the current breeding season (different lines).

7 Model validation and sensitivity analysis

Once the parameters of the spring migration model have been estimated, the model can be used (via forward simulations) to make predictions on the following aspects of the migration schedule:

- The pattern of site use, i.e. which sites are used and which sites are skipped (migration route)
- The timing of site use, i.e. when do the birds arrive and when do they depart from the sites that are included in the migration schedule
- Arrival mass and departure mass at each stopover site
- Timing and condition at arrival on the breeding grounds
- The proportion of birds that die on migration
- The proportion of birds that survive, but fail to reach the breeding grounds
- The reproductive success achieved on the breeding grounds

These predictions cannot be directly derived from the data used to estimate the parameters so we can use these predictions to validate the model. For Knots, detailed data are available on the pattern and timing of site use (see Chapter 3) and these are therefore the primary data to validate the model. Data on arrival mass and departure mass on the staging sites were also available in considerable detail (see Chapter 3), but time did not permit a detailed analysis.

In contrast, data on timing and condition at arrival on the breeding grounds, reproductive success, non-breeding and survival during spring migration, are scarce to non-existent for Knot. There are estimates of mortality of Knot (Boyd & Piersma 2001), but these apply to the annual cycle as a whole, not only to spring migration. Thus, these predictions are more easily tested using an annual model.

We also used this model output to perform a sensitivity analysis to test which parameters had the greatest effect on the pattern and the timing of migration. However, we did not restrict the sensitivity analysis to aspects of the migration schedule that could be validated, but also included survival during migration.

7.1 Parameter estimates

A first step for both validation and sensitivity analysis is to specify the parameter values. In the preceding chapters we described the equations and the parameters and how we arrived at best estimates for each of the parameters in the migration model. The actual values of “global” parameters for the two subspecies of Knot are given in Table 7-1.

Table 7-1. Parameter values used in the sensitivity analysis for the two subspecies of Knot, i.e the Siberian subspecies *canutus* which migrates between Siberia and Africa, and the Icelandic subspecies *islandica*, which migrates between estuaries in NW Europe and Greenland and the Canadian arctic.

Parameter	Symbol	<i>Cc canutus</i>	<i>Cc islandica</i>
Maximum body stores	x_{\max}	100	100
Range body mass		110-210 g	110-210 g
Max. energy load		3277 kJ	3277 kJ
Time horizon	T	180 d	180 d
Stop-over sites	$i \dots N$	7	6
Distance between sites	D_{ij}	see Table 3-6	see Table 3-3
Flight speed		1440 km/ d	1440 km/ d
Flight range	C	11677 km	11677 km
Terminal reward	$F(x,t,N)$		
- Reproductive success	$R(t)$ $\alpha_0, \alpha_1, \alpha_2$	1.02, 127.94, 18.025	2.2, 115.96, 26.928
- Survival	$S(x, t)$ s_0, s_1, s_2	32.1, 0.2506, 0.0873	28.61, 0.246, 0.065
- expected future reproductive success	B_0	3.2	3.0
Predation risk			
- mass-dependent exponent	A	4.0	4.0
- foraging intensity- dependent exponent	B	4.0	4.0

Site-dependent parameters for the two subspecies of Knot are given in Table 7-2 for the Siberian subspecies *Calidris c. canutus* and in Table 7-3 for the Icelandic subspecies *Calidris c. islandica*. The parameters m_0 , m_γ , and m_β are baseline predation risk and coefficients for foraging and mass-dependent predation risk, respectively (see equation 2.4 in Chapter 2).

Table 7-2. Site-dependent parameters for *C.c. canutus*.

Parameter	Symbol	S0	S1	S2	S3	S4	S5	S6
Predation risk Baseline	m_0	1.0E-4	1.0E-4	1.0E-4	1.0E-4	1.0E-4	1.0E-4	1.0E-4
foraging intensity-dependent	m_γ	1.0E-2	1.0E-2	1.0E-2	1.0E-2	1.0E-2	1.0E-2	1.0E-2
mass-dependent	m_β	1.0E-3	1.0E-3	1.0E-3	1.0E-3	1.0E-3	1.0E-3	1.0E-3
Intake rates	$g(i,t)$	9.2	6.15	7.16	10.5	12.6	14.3	13.7
Stochasticity in intake rates		1.0	1.0	1.0	1.0	1.0	1.0	1.0
Expenditure on site i at time t (x/ day)	$e(i,t)$	0 6.9 15 6.8 43 7.1 74 7.6 104 8.2 135 8.7 165 8.9 180 8.9	0 5.7 15 5.5 43 5.3 74 5.3 104 5.2 135 5.1 165 5.4 180 5.4	0 6.9 15 6.8 43 6.5 74 6.5 104 6.2 135 5.9 165 5.9 180 5.7	0 10.6 15 10.5 43 10.0 74 9.4 104 8.5 135 7.7 165 7.1 180 7.2	0 11.9 15 11.8 43 11.2 74 10.3 104 9.1 135 8.3 165 7.9 180 7.9	0 13.5 15 13.5 43 13.0 74 12.3 104 11.3 135 10.3 165 9.5 180 9.6	0 15.2 15 15.0 43 13.7 74 12.2 104 10.7 135 9.1 165 8.3 180 8.5

Table 7-3. Site-dependent parameters for *C.c. islandica*.

Parameter	Symbol	S0	S1	S2	S3	S4	S5
Predation risk Baseline	m_0	1.0E-4	1.0E-4	1.0E-4	1.0E-4	1.0E-4	1.0E-4
foraging intensity-dependent	m_γ	1.0E-2	1.0E-2	1.0E-2	1.0E-2	1.0E-2	1.0E-2
mass-dependent	m_β	1.0E-3	1.0E-3	1.0E-3	1.0E-3	1.0E-3	1.0E-3
Intake rates	$g(i,t)$	12.7	12.6	11.7	12.6	13.7	14.3
Stochasticity in intake rates		1.0	1.0	1.0	1.0	1.0	1.0
Expenditure on site i at time t (x/ day)	$e(i,t)$	0 10.7 15 10.7 43 10.4 74 10.0 104 9.3 135 8.7 165 8.2 180 8.2	0 11.6 15 11.5 43 11.0 74 10.2 104 9.1 135 8.4 165 8.0 180 8.0	0 10.9 15 10.9 43 10.5 74 10.0 104 9.3 135 8.6 165 8.1 180 8.1	0 11.9 15 11.8 43 11.2 74 10.3 104 9.1 135 8.3 165 7.9 180 7.9	0 12.4 15 12.3 43 12.2 74 11.5 104 10.7 135 9.9 165 9.5 180 9.6	0 13.5 15 13.5 43 13.0 74 12.3 104 11.3 135 10.3 165 9.5 180 9.6

7.2 Model validation and Sensitivity analysis

A sensitivity analysis identifies key factors by estimating and comparing the effects of changes in parameters and thereby calculates the proportional contribution of a particular parameter to an output measure, e.g. survival (Jorgensen & Bendoricchio 2001; Caswell 2000). We conducted a sensitivity analysis of the spring migration model by changing the standard parameter values by $\pm 20\%$. This procedure has been repeated for every parameter independently in a step-wise fashion. Thereafter, we

compared the results of the model using the changed parameters with model predictions from the standard parameter set both qualitatively and quantitatively. Qualitative assessment included differences in the migration route followed and for the quantitative assessment of differences we calculated the elasticities E of each parameter on several output measures, i.e. staging times on each site and survival:

$$E = \frac{R_{P_{\min}} - R_{P_{\max}}}{R_{P_{\text{standard}}}} \bigg/ \frac{P_{\min} - P_{\max}}{P_{\text{standard}}}$$

with $P_{\min, \max, \text{standard}}$ the minimum, maximum and standard value of the parameter and $R_{P_{\min, \max, \text{standard}}}$ the result obtained when using the respective parameter value. This procedure allowed us to identify the parameters that considerably change the output, i.e. have an elasticity different from 0.0. This type of sensitivity analysis is generally referred to as an elasticity analysis (Heppell *et al.* 2000; de Kroon *et al.* 2000). Since the birds may start their spring migration from different wintering areas and since the breeding area covers a large tract of tundra, we repeated the elasticity analysis for different starting and breeding locations.

7.2.1 Results *Cc canutus* – migration routes

7.2.1.1 Actual migration

Detailed information on the migration of *Cc canutus* is provided in chapter 3.2. The birds belonging to this subspecies typically migrate from wintering grounds in South Africa, Guinea Bissau and Mauritania via the Wadden Sea to their breeding grounds in Taimyr (Figure 7-1). However, when encountering head winds, they use an additional stop-over site in France. A similar phenomenon may occur in the White Sea, where flocks of up to a few thousand birds have been observed, but which does not seem to be a regular staging site for the bulk of the population.

7.2.1.2 Model results

In the model, we found that *Cc canutus* typically migrate from the wintering grounds via France, the Wadden Sea and the White Sea to the breeding grounds (Figure 7-1). However, another typical pattern appeared when using a different breeding location. Birds migrate from the wintering ground via France, the Wadden Sea and Norway, instead of the White Sea, to the breeding grounds. Furthermore, no bird wintering in South Africa managed to cover the distance to the closest stop-over site (Guinea Bissau), indicating that the birds in reality either depart with substantial wind assistance or make use of intermediate stopover sites. We also found that birds in the model always stopped in France and again stopped either in Norway or the White Sea. The birds never flew directly from the Wadden Sea to Taimyr. According to empirical observations, landing in France only occurs in substantial numbers when the birds encounter considerable head winds during migration and numbers stopping

over in the White Sea are probably small, though poorly known. This subspecies is considered a vagrant in northern Norway. Again, this suggests that wind assistance is an important factor that cannot be ignored.

Changing parameter values in the elasticity analysis led to changes in the typical migration routes such that birds typically stopping in Norway now skipped this site and stopped in the White Sea instead (and vice versa). Parameters responsible for such switches of stop-over sites were intake rates and predation risk in Norway and the White Sea, while changing parameters in the other sites had no such effect.

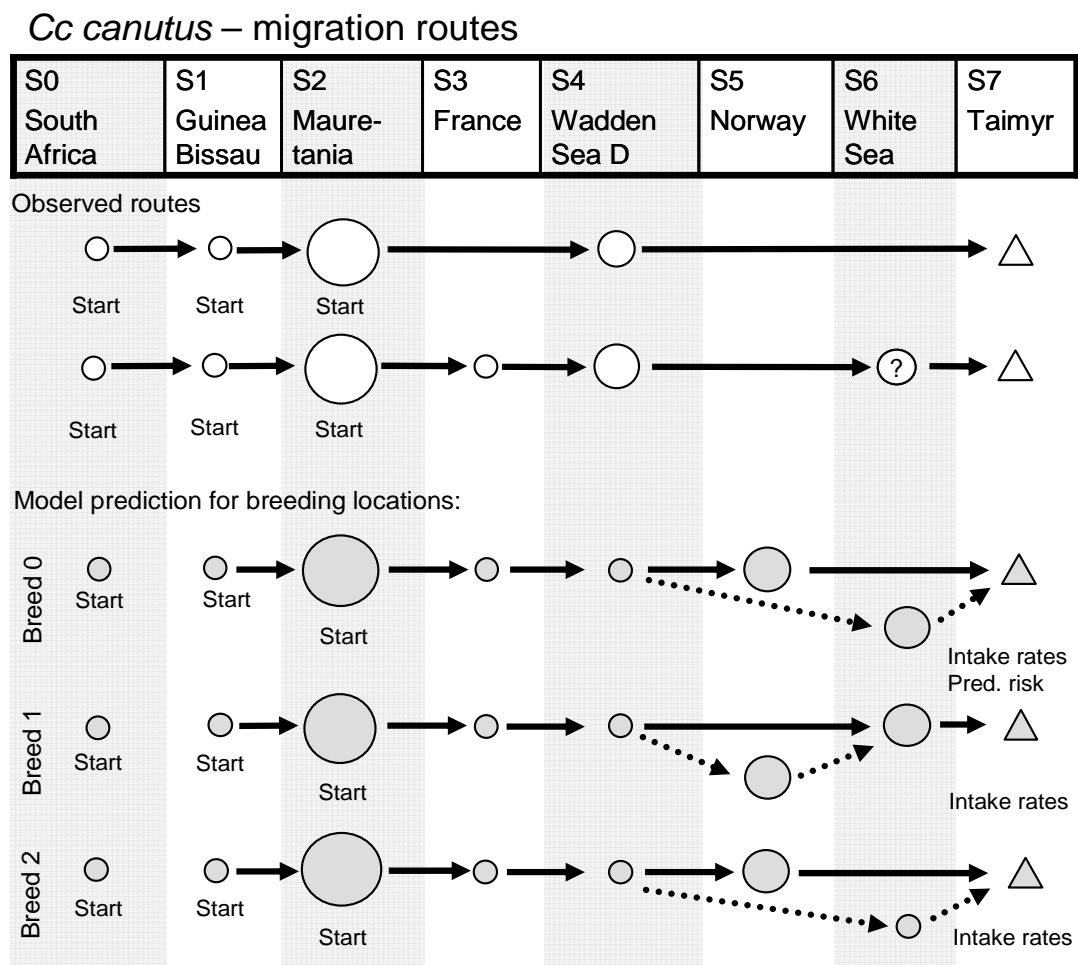


Figure 7-1. Observed and predicted migration routes of *Cc canutus*. Circles indicate stop-over sites used during migration and the size of the circles give the relative staging time. Three different breeding locations have been used in the model, where Breed 0 refers to location 75N89E (West Taymyr), Breed 1 to 73N80E (Dikson), and Breed 2 to 75N113E (East Taymyr).

7.2.2 Results *Cc islandica* – migration routes

7.2.2.1 Actual migration

Detailed information on the migration of *Cc islandica* is provided in chapter 3.1. *Cc islandica* uses four typical migration routes from their wintering grounds in France, NL or UK to reach their breeding grounds in Greenland and the Canadian Arctic. Between the wintering and breeding grounds, there are an early and a late-spring stop-over sites. The early-spring site is either in the German Wadden Sea or in Morecambe Bay in West-Britain. The late-spring staging site is either Iceland or Norway. The migration routes result from four combinations of these early and late-spring sites; however, there is a clear difference in the number of birds using a particular route (Figure 7-3).

It has been hypothesized that birds breeding in North and North-East Greenland use the Norwegian route and birds breeding in the Canadian archipelago the Icelandic route.

7.2.2.2 Model results

Irrespective of where the birds winter, i.e. France, Dutch Wadden Sea or UK, they typically migrate via the German Wadden sea and Norway to breeding grounds in East Greenland (70N22W), which we indicated as breeding area 0 (Figure 7-2). Changes in intake rates in the German Wadden Sea made the birds to avoid this site and rather change their route to either include an additional stop in Iceland or increase the length of their stay in Norway.

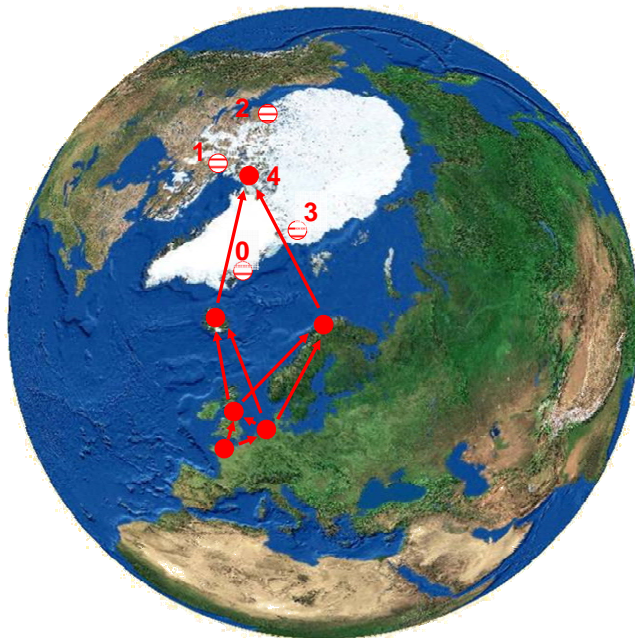


Figure 7-2: Location of the various breeding areas of *islandica* Knots used in the forward simulations.

Cc islandica – migration routes

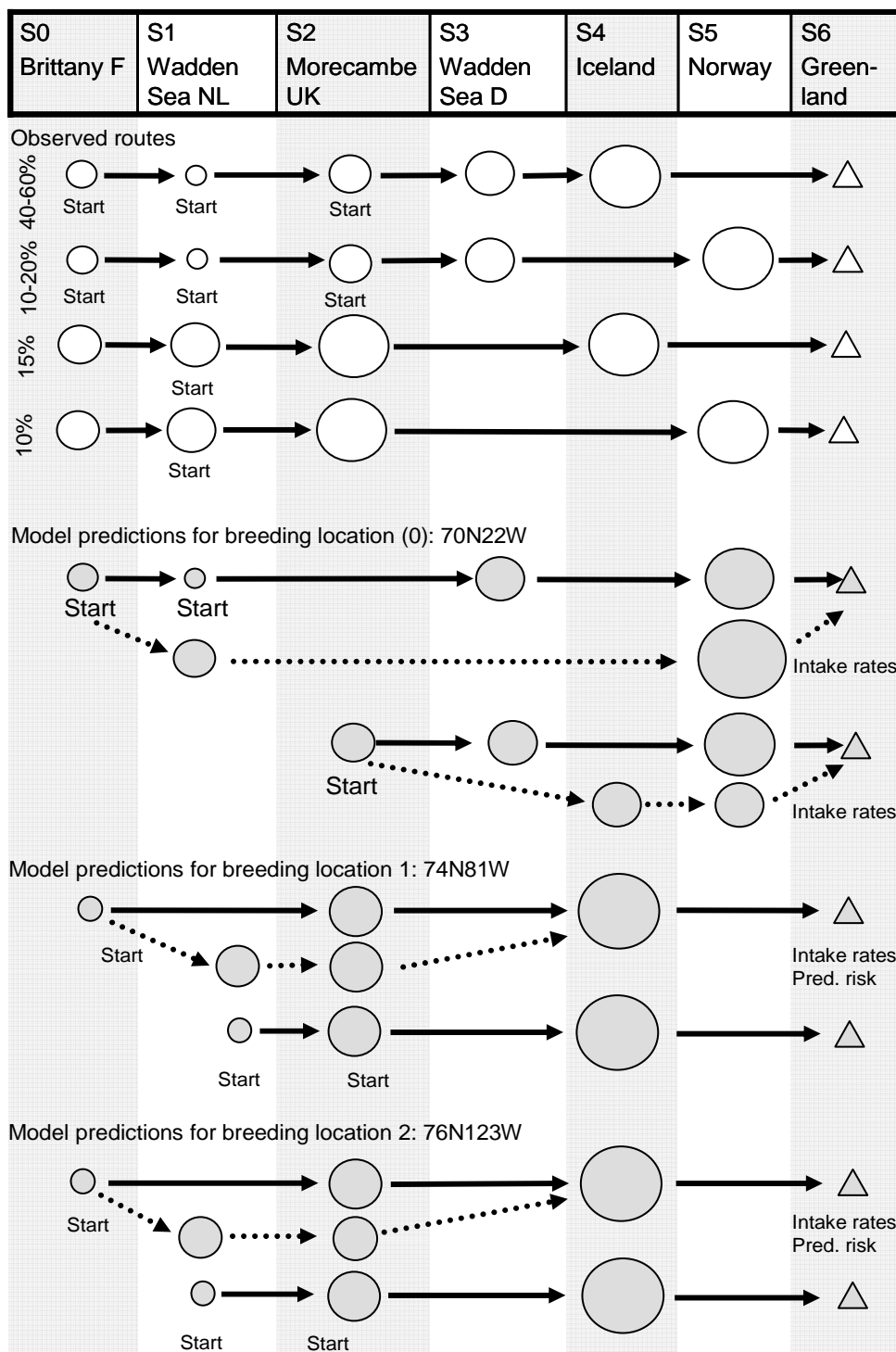


Figure 7-3. Observed and predicted migration routes of *Cc islandica*. Circles indicate stop-over sites used during migration and the size of the circles gives the relative staging times. Five different breeding locations have been used in the model, where location 0 refers to 70N22W (East Greenland), location 1 to 74N81W (Baffin Island), location 2 to 76N123W (Banks Island), location 3 to 81N12W (NE Greenland), and location 4 to 80N70W (Ellesmere Island).

The predicted typical migration route for the East Greenland breeding location (Breed 1 - 74N81W) is via Morecambe UK and Iceland to the breeding grounds (Figure 7-3). However, if predation risk or intake rates change, birds may additionally use the German Wadden Sea as stop-over site.

Cc islandica – migration routes

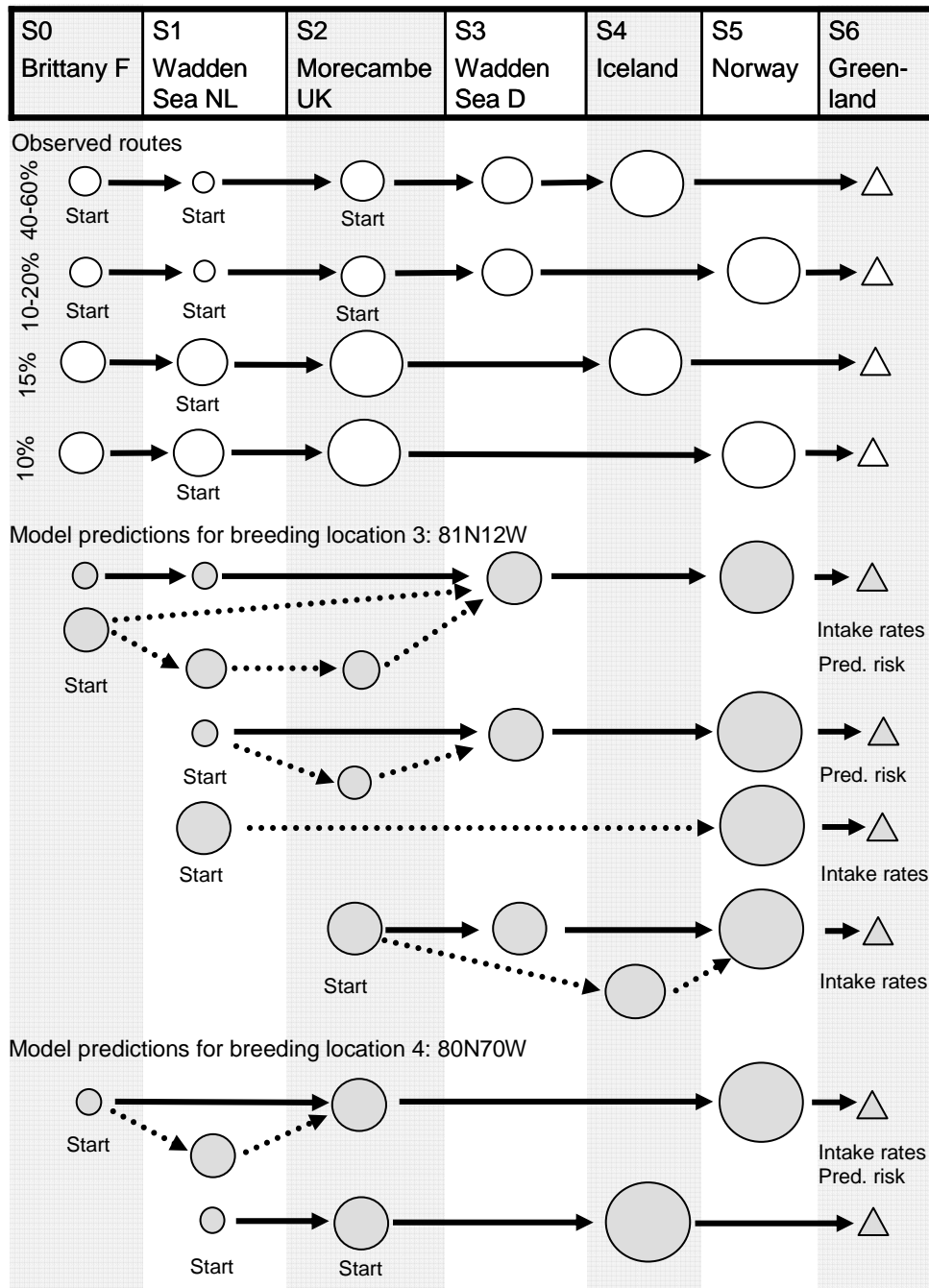


Figure 7-4 – continuation of Figure 7-3.

Birds heading for the Banks Island breeding location in Canada (Breed 2 - 76N123W) use the route via Morecambe UK and Iceland as default and irrespective of wintering location (Figure 7-3). However, changes in intake rates and predation risk lead to the additional use of the German or the Dutch Wadden Sea.

The default route to the North-East Greenland breeding location (Breed 3 - 81N12W) is via the German Wadden Sea and Norway. Changing intake rates and predation risk led to the additional use of Morecambe UK or Iceland (Figure 7-4).

Birds heading for breeding grounds on Ellesmere Island (Breed 4 - 80N70W), migrated from either wintering location via Morecambe UK and Norway to the breeding grounds (Figure 7-4). Again, changing intake rates and predation risk led to the additional use of the Dutch Wadden Sea.

The interesting pattern that emerges is that birds breeding in Canada are generally predicted to migrate via Iceland, whereas the birds breeding in Greenland are predicted to migrate via Norway. This pattern seems quite robust to changes in parameter values. For birds breeding on Ellesmere Island, in between the Greenland breeding locations and the more westerly Canadian breeding locations, the wintering site determines whether they use Norway or Iceland as stopover.

7.2.3 Staging times

In the field, the following staging and departure times from the sites have been observed for *Cc canutus* (numbers in parentheses give day numbering in the model): South Africa 15-20 April (day 74 – 79), Mauritania late April till 10 May (day 80 – 99), Wadden Sea 1-9 June (day 121 – 129).

Cc islandica has been observed to arrive and depart from the stop-over sites at the following periods: arrival at Morecambe UK and/ or German Wadden Sea mid to late March (day 43 – 59), and departure from there in the first two weeks of May (day 90 – 105); arrival in Iceland late April till first week of May and in Norway first two weeks of May. Departure from the latter two sites is 25 May – 1 June (day 114 – 121).

For both populations, the model predicted earlier departures from the early-spring staging sites than those observed in reality (Figure 7-5). This deviation most likely results from errors in our estimations of site-specific parameters. Our present estimates of site-specific intake rates does not include seasonal changes in prey availability for instance. We derive our estimate of maximal daily intake rates from fattening rates achieved during the period of the season that the site is actually used (see chapter 3) and assume the same intake rates can be achieved at other times of the year. This is unlikely to be true. Northern staging sites may not be snow- or ice-free early in the spring, and even in a temperate site such as the Wadden Sea, the availability (burying depth) and quality (ratio of flesh mass to shell mass) of the bivalves that Knots feed upon are known to increase during spring (Zwarts & Wanink 1993). In our model, the amount of energy that can be used for fattening is found by subtracting the costs of maintenance metabolism and it is only these costs

that are assumed to vary in the course of the season as a result of changes in ambient temperature (Figure 4-3). With regard to predation risk we have no proper estimates, let alone seasonal changes in risk. Additionally, there is considerable variation in empirical departure dates and usually, they are only known as population rather than individual values. However, the model predictions for both departure times from late spring staging sites and arrival in the breeding grounds were well within the empirically observed range.

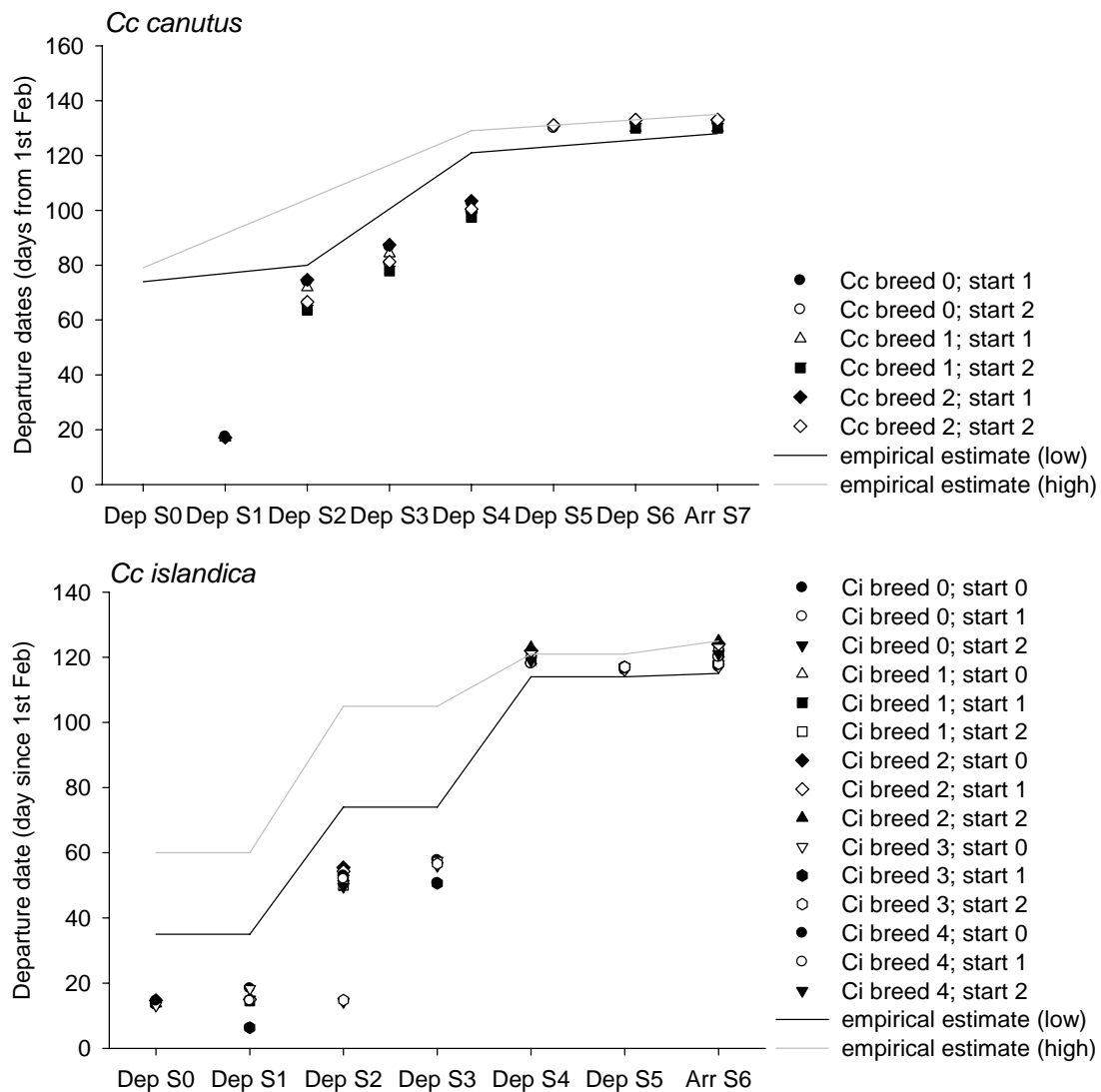


Figure 7-5. Departure dates from the stop-over sites as predicted by the standard model scenarios using the potential wintering ('start') and breeding ('breed') locations (symbols) and as observed in the field (grey and black lines are respectively upper and lower boundaries in the distribution) for *Cc canutus* (upper panel) and *Cc islandica* (lower panel). In general, there is good agreement between predicted and observed departure dates in the 'late' staging sites and the arrival in the breeding grounds but less so for the 'early' sites and the departure from the wintering grounds.

7.2.4 Elasticity of survival rates and staging times

Survival was generally high in all scenarios and ranged between 90-100%. Parameters which led to increased mortality during spring migration were predation risk and intake rates on those sites, on which the birds stayed longest. Accordingly, the site-specific parameters with the greatest influence on staging times have also been identified to include predation risk and intake rates (Table 7-4, Table 7-5). Interestingly, the 'late' sites tend to be less affected by parameter changes compared to the early sites, i.e. have generally lower elasticity values.

Table 7-4 Results of the elasticity analysis for staging times of Cc canutus. For each staging site, up to five parameters are listed, for which elasticities clearly departed from 0.0 and which are thus most influential for staging times. Rows contain the results from the different wintering ('start') and breeding ('breed') location scenarios.

Staging times	S1	S2	S3	S4	S5	S6
Cc 01 Breed 0 Start S1	S1_b1 S1_yGain Pred_a1 S1_pGain S5_yGain	S2_yGain S2_b1	S3_yGain S3_b1	S4_yGain S4_b1	S5_b1 S5_yGain S6_yGain S6_b2 Surv_a0, a1	
Cc 02 Breed 0 Start S2	----	S2_yGain CRS_a1 S4_yGain	CRS_a1 S3_yGain S3_b1	S4_yGain S2_yGain CRS_a1 S4_b1	S5_b2 S6_b2 S5_yGain S6_yGain	
Cc 11 Breed 1 Start S1	S1_yGain CRS_a1 S2_yGain S1_b1	S2_yGain S2_b1	S3_yGain S3_b1	S4_yGain S4_b1 S2_yGain CRS_a1 S6_yGain		Surv_a0 Surv_a1 S6_yGain S5_yGain CRS_a1
Cc 12 Breed 1 Start S2	----	S2_yGain S2_b1 CRS_a1	CRS_a1 S3_yGain S3_b1	S4_yGain S2_yGain CRS_a1 S4_b1 S2_b1		Surv_a0 Surv_a1 S6_yGain S5_yGain CRS_a1
Cc 21 Breed 2 Start S1	S1_yGain CRS_a1 S1_b1 Pred_a1 Pred_a2	S2_yGain CRS_a1 S2_b1 Surv_a0	S3_yGain CRS_a1 S3_b1 Surv_a0	S4_yGain S2_yGain S4_b1 CRS_a1 Surv_a0	S5_yGain Surv_a0 S5_b1 Pred_a1 Speed	
Cc 22 Breed 2 Start S2	----	S2_yGain CRS_a1 Surv_a0 S2_b1	S3_yGain CRS_a1 S3_b1 Surv_a0	S4_yGain S2_yGain CRS_a1 S4_b1 S2_b1	S5_yGain Surv_a0 S2_yGain S5_b1 Pred_a1	

Table 7-5 Results of the elasticity analysis for staging times of *Cc islandica*. For each staging site up to five parameters which greatly influenced staging times are listed. Rows contain the results from the different starting and breeding location scenarios.

Staging times	S0	S1	S2	S3	S4	S5
Ci 00 Breed 0 Start S0	C S1_yGain	S1_yGain S3_yGain S1_b1 S3_b1 Pred_a1		S3_yGain S1_yGain		S3_yGain
Ci 01 Breed 0 Start S1		S1_yGain S3_yGain S1_b1 S3_b1 Pred_a1		S3_yGain S1_yGain		S3_yGain
Ci 02 Breed 0 Start S2						
Ci 10 Breed 1 Start S0	S2_yGain CRS_a1 S0_b1 S2_b1 S2_yGain		CRS_a1 S1_yGain S2_yGain S0_yGain C		S4_yGain Surv_a0 Surv_a1 Pred_a1 S1_yGain	
Ci 11 Breed 1 Start S1		S2_yGain S1_yGain S1_b1 S2_b1 CRS_a1	S2_yGain S1_yGain CRS_a1 C Pred_a1		S4_yGain Pred_a1 Pred_a2 Surv_a1	
Ci 12 Breed 1 Start S2			CRS_a0 S4_yGain S2_yGain Surv_a0 Surv_a1		S4_yGain S2_yGain Pred_a1 Pred_a2 Surv_a0	
Ci 20 Breed 2 Start S0	S2_yGain S2_b1 S0_b1 Pred_a1 S0_yGain		S1_yGain S4_yGain S0_yGain Pred_a2 S2_yGain		S4_yGain Pred_a1 Pred_a2	
Ci 21 Breed 2 Start S1		S2_yGain S2_b1 S1_b1 S1_yGain S4_yGain	S1_yGain S2_yGain S1_b1 S2_b1 Pred_a1		S4_yGain Pred_a1	
Ci 22 Breed 2 Start S2			S4_yGain Pred_a1 Pred_a2 S2_yGain S4_b1		S4_yGain Pred_a2 Pred_a1 S2_yGain	
Ci 30 Breed 3 Start S0	S1_yGain S3_yGain	S1_yGain S3_yGain S1_b1 S3_b1 S0_yGain		S3_yGain S1_yGain c		S3_yGain S1_yGain Surv_a0 Surv_a1
Ci 31 Breed 3 Start S1		S3_yGain S1_yGain S3_b1		S3_yGain S1_yGain C		S3_yGain S5_yGain c

Staging times	S0	S1	S2	S3	S4	S5
		S1_b1 CRS_a1		CRS_a1		
Ci 32 Breed 3 Start S2			S3_yGain S2_yGain Pred_a1 CRS_a1 Pred_a2	S3_yGain CRS_a1 S5_yGain		S3_yGain S5_yGain Surv_a0 Surv_a1
Ci 40 Breed 4 Start S0	S2_yGain S0_yGain CRS_a1 S0_b1 S2_b1		S2_yGain S4_yGain S1_yGain C CRS_a1		S4_yGain S2_yGain Pred_a1	
Ci 41 Breed 4 Start S1		S2_yGain S1_yGain S1_b1 S2_b1 CRS_a1	S2_yGain S1_yGain S4_yGain S2_b1 S1_b1		S4_yGain Surv_a0 Surv_a1	
Ci 42 Breed 4 Start S2			S4_yGain S2_yGain Pred_a1 Pred_a2 CRS_a1		S4_yGain S2_yGain Pred_a1 Pred_a2	

8 Discussion and conclusions

When we started our investigations several years ago, we concluded that for shorebirds the terminal reward was probably the most influential function in the dynamic migration model developed by Weber *et al.* (1998), yet there were no empirical data to estimate the parameters of this function. Thus, we spent much effort in expeditions to the high arctic tundra to empirically study the relationship between condition and time of arrival at the breeding grounds and subsequent reproductive success. These investigations proved highly successful, even though the direct approach to the estimation of the terminal reward that we originally envisaged did not work. It proved impossible to catch shorebirds upon arrival to mark them and measure condition and subsequently measure their reproductive success in sufficient numbers. Luckily, we could develop an indirect approach. Growth of shorebird chicks was found to depend on insect availability and insect availability was found to depend on temperature, season and “depletion” (when the weather has been favourable for several days in a row it appears that the pool of insects that can emerge is “depleted”). This relationship allowed us to reconstruct the feeding conditions for the chicks on the basis of past weather data. Assuming that a shorebird about to depart on migration cannot predict the weather on the breeding grounds during the breeding season to come, we could calculate for each arrival time the number of chicks the bird could expect to fledge. To complete the picture, we also estimated the risk of starvation for a given arrival mass and a given arrival time (birds that arrive too early encounter a frozen tundra), as well as the future reproductive success for birds that survived till the end of the breeding season, irrespective of whether they raised a clutch or not. Our empirical investigations were focused on Taimyr, but we extrapolated the results to Greenland. To feel more secure about this kind of extrapolation, measurements on weather, insect availability and chick growth are needed for a variety of shorebird species on a range of locations spread over the entire arctic. This is one of the items that we will address if our project proposal for the International Polar Year 2007-2008 gets funded (see Appendix 3).

Having successfully targeted the weakest link in the modelling made us aware of the next weakest links. Three issues stand out:

- **Risk of predation.** There is abundant information that shorebirds at times run a substantial risk of predation. Thus, it is likely that the risk of predation is a major factor shaping the migration schedules of shorebirds. However, there is almost no information that allows us to link this predation risk to the decisions made by the birds during migration. We need estimates of differences in predation risk between sites and between different times in the season and we need to know the relationship between feeding decisions and predation risk. There is a clear need for empirical studies on this subject.
- **(Variable) weather conditions en route.** Our modeling efforts neither included the wind conditions en route, nor the variability in these wind conditions. However, without tailwinds migrations exceeding 3400 km are

not possible in a single leap, yet Knots are known to perform such migrations. Including realistic wind conditions will solve this problem. This will also mean that variability in wind conditions will be included and this will have the following additional effects: (1) departure mass will be higher, because a safety margin is needed in case unfavourable winds are encountered on the way, (2) travel time will probably increase, because more fuel has to be accumulated at each stopover site.

- **Seasonal changes in the feeding conditions at each stopover site.** Our present estimates of site-specific intake rates do not include seasonal changes in prey availability. We derive our estimate of maximal daily intake rates from fattening rates achieved during the period of the season that the site is actually used (see chapter 4) and assume the same intake rates can be achieved at other times of the year. This is unlikely to be true. Northern staging sites may not be snow- or ice-free early in the spring, and even in a temperate site such as the Wadden Sea, the availability (burying depth) and quality (ratio of flesh mass to shell mass) of the bivalves that Knots feed upon are known to increase during spring (Zwarts & Wanink 1993).

In general, migration routes were correctly predicted, but there were also notable discrepancies, especially for the subspecies *canutus*: (1) Knots of this subspecies wintering in South Africa probably migrate in a single leap to Guinea-Bissau, but the model Knots could not reach Guinea-Bissau in a single leap, (2) Knots of this subspecies migrating northward from the Banc d'Arguin usually fly to the Wadden Sea in a single leap, but the model Knots always landed in France, (3) Knots of this subspecies migrating northward from the Wadden Sea are believed to fly directly to their Siberian breeding grounds, but the model Knots always landed in northern Norway. It could be that our estimates of flight costs are too high, but we think this unlikely. Instead, the Knots probably rely on tailwinds. Including realistic (and thus variable) wind conditions will probably solve this problem.

In contrast, the simulation results for the migration schedule of the Knot subspecies *islandica*, which breeds on Greenland and northern Canada and winters in NW Europe, were especially encouraging. The majority of this population uses Iceland as a stopover site, but a minority (20-30%) migrates via northern Norway. A sensitivity analysis indicated that birds breeding in the more westerly parts of the Canadian breeding range should migrate via Iceland, whereas the birds breeding on Greenland should migrate via northern Norway. Whether birds breeding on Ellesmere Island (in between Greenland and the more westerly part of the Canadian breeding range) migrate via Norway or Iceland depends on their wintering area according to the model. At present, there are insufficient data to test this prediction. Wilson & Strann (2005) observed many colour-marked Knots in northern Norway, but only two of these were marked on the breeding grounds: Ellesmere Island.

The predictions for the timing of site use were also partly correct and partly wrong. Forward simulations showed that the birds always arrived on time. However, the birds departed too early from the wintering sites and migrated too slowly. This was

true for both subspecies and for all combinations of starting location and breeding area. Several possible explanations for this discrepancy exist:

- We estimated maximal fattening rates from published values of fattening rates, based on population averages. Perhaps the true maximum is higher.
- Our current model may overestimate the attractiveness of northerly sites early in the season – as stated before, our current model does not include changes in prey availability and prey quality in the course of the season.
- The costs, in terms of increased predation risk, of fattening quickly and/or the baseline predation risk of southern sites may be overestimated.
- As stated before, we did not include wind conditions. Perhaps, wind conditions are unfavourable early in the season, and favourable tailwinds are only present later in the season.

A sensitivity analysis of survival rates showed that survival rates predicted by the model generally varied between 90-100%. These figures seem reasonable for a long-lived species like the Knot: Boyd & Piersma (2001) report annual adult mortality rates for three different periods that vary between 14.2% in 1985-95 to 23.6% in 1969-77. More precise tests are not possible at present, because we lack empirical estimates of survival that apply to only part of the season.

In 1997, we organized an international workshop to try to link the dynamic migration model developed by Weber *et al.* (1998) to the real world, i.e. to investigate the applicability of the model to well-studied avian migration routes of some shorebirds and geese. We are encouraged by the progress that we made since then with regard to the migrations of geese and swans (Beekman *et al.* 2002; Klaassen *et al.* 2006; Bauer *et al.* 2005) and shorebirds (this report), even if there are still details that do not fit. Such details define a clear research agenda, which we already discussed and which we will summarize in the final chapter with recommendations. However, the prime concern of the policy makers who funded our research is not with research agendas, but with applications. For Knots we are now in a good position to repeat the general calculations of Weber *et al.* (1999) on the effects of habitat loss or habitat degradation at migratory stopover sites. It is also possible to use the model to study some of the effects of climate change. Global climate change may affect migratory shorebirds both in their winter and migration stopover sites (sea level rise, availability of intertidal habitats), during the migratory flights (wind conditions) and in the breeding range (climatic breeding conditions, vegetation belts). Clearly, some of these effects, like the effects of wind conditions, are not yet included in the model. This is one of the items that we will address if our project proposal for the International Polar Year 2007-2008 gets funded (see Appendix 3).

Policy makers are not interested in only one species of shorebird, but in all species that frequent the Wadden Sea and the Delta area in large numbers. For this reason, we collected information on the migration routes of seven different shorebird species in all. However, lack of data forced us to focus all our subsequent efforts on the two subspecies of Knot (van Gils 2004). Given the lack of information on the other species, the most profitable way to proceed may be to investigate how differences in body size would affect the predictions that can be derived for Knots. The various

species differ in more aspects than body size, but body size is an important variable that affects many, if not all, physiological and ecological processes (Calder III 1984; Kooijman 1993). For shorebirds, there is literature available describing how energy needs (Kersten & Piersma 1987; Klaassen *et al.* 1990) and fuel deposition rates (Lindström 2003) depend on body size.

Whatever improvements we make to DYNAMIG, two facts will remain. The model only applies to spring migration and it calculates the optimal decisions for “isolated” individuals. This means that predicted effects apply to the fitness expectations of individuals. From this, population consequences have to be inferred. More recently, migration has been modelled within the context of an annual routine (McNamara *et al.* 1998). The annual model not only covers the entire annual cycle, but also includes density dependence, which is either implicitly incorporated (McNamara *et al.* 1998), or modelled explicitly (Bauer, unpublished). Thus, contrary to the spring migration model, individuals are not considered in isolation, but competing with each other for scarce resources, like food on staging sites, or territorial space on the breeding grounds. This means that the model is able to directly predict population consequences of climate change or habitat change on stopover sites. Many parameters (energetic demands, flight costs, risk of predation etc.) are the same in both models. Thus, much groundwork has already been done. This is one of the items that we will address if our project proposal for the International Polar Year 2007-2008 gets funded (see Appendix 3).

9 Recommendations

In this chapter we briefly summarize the recommendations made previously:

- Test the prediction that Knots breeding in Canada migrate via Iceland and that Knots breeding in Greenland migrate via Norway
- Investigate if our method to construct the terminal reward from weather data can also be applied to other areas in the arctic and to other shorebird species
- Improve the spring migration model (DYNAMIG) by
 - Proper inclusion of variable wind conditions *en route*
 - Obtaining better empirical estimates of predation risk
 - Proper inclusion of seasonal changes in prey availability and prey quality
- Parameterize the spring migration model for other shorebird species
- Use spring migration model for scenario calculations on the effects of climate change and habitat loss or degradation on stopover sites
- Extend the DYNAMIG model to the full annual cycle and include density dependence

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Appendix 1 - Activities in the project

Year 2002

Empirical research on the terminal reward function:

- For the third year running (2000-2001 within the previous programme, 330), an expedition was made to the Willm Barentz Biological Station near Dickson, Taimyr, Russia. From 8 June to 11 August we studied the breeding biology of shorebirds that reproduce in the Russian tundras and winter in Europe, Africa and Asia. Our studies aim at identifying fitness consequences of arrival date and arrival condition, which provide a link between events occurring in the winter and migratory stopover areas of the birds, and their reproductive success. These consequences determine the shape of the 'terminal reward function' in the mathematic models of bird migration which are developed in the second workpackage. After two years of low lemming abundance and high predation rates on shorebird eggs and chicks, lemmings were on the increase in 2002 and predation rates were moderate, allowing easier collection of data. We collected data on shorebird body condition in different stages of the breeding cycle and upon arrival and departure, arrival date and return rates in Dunlin *Calidris alpina*, laying date, clutch size and egg size of all shorebird species, nest success, occurrence of replacement clutches, energy expenditure during incubation and chick-rearing (Dunlin), growth rates of shorebird chicks, and patterns in abundance of surface-active arthropods. Additionally, this year we studied nest insulation in different shorebird species, time allocation to incubation and foraging in relation to food availability in Little Stints *C. minuta*, and time and energy budgets of growing Little Stint chicks. Thanks to the lower predation rate, we were able to collect much data especially on chick development and energetics, a valuable addition to the work of previous years. In total we ringed over 600 shorebirds and received three foreign recoveries linking our study site to passage and wintering sites in W-Europe and Africa: Curlew Sandpipers *C. ferruginea* from Spain and South Africa, and a Little Stint from Namibia.
- After returning to The Netherlands, data input and analysis was taken up to produce a report summarising this season's findings and basic data, as in previous years. This report was finalised in December 2003.
- Progress was made with several publications for peer-reviewed scientific journals: two manuscripts were submitted for publication, a third was accepted for publication in *Oecologia*, and a fourth appeared in *The Ibis* in 2002.
- Lectures on the research project were given for audiences of amateur ornithologists in Groningen and Friesland

Extending the DYNAMIG model:

- Discussions with Marcel Klaassen at the NIOO on the best way to proceed with the DYNAMIG model
- Participated in examining applications for a modeller that will be appointed at the NIOO to apply DYNAMIG to geese and swans.
- Attended the behavioural ecology symposium in Montreal

Year 2003

- In 2003 no expedition was carried out. All funds available were allocated to analysing and writing up the data collected during the field seasons of 2000-2002 at the Willem Barentz Biological Station near Dickson, Taimyr. Our studies aim at identifying fitness consequences of arrival date and arrival condition, which provide a link between events occurring in the winter and migratory stopover areas of the birds, and their reproductive success. These consequences determine the shape of the 'terminal reward function' in the mathematic models of bird migration, which are developed in workpackage B.
- Progress was made with several publications for peer-reviewed scientific journals: two manuscripts were submitted for publication, one was published in *Oecologia* and one in *Functional Ecology* in 2003. One paper was published in the bulletin of the wader Study Group. Two manuscripts are in an advanced state and will be ready for submission in spring 2003.
- Apart from the scientific papers, a popular scientific paper was written for a Dutch Bird Journal and will be published in spring 2004.
- After finalizing the expedition report of the third field season (2002), a report integrating the results of the three expeditions is being prepared and will be finalized in spring 2004.
- Three different oral presentations on the research project were given at the conference of the European Ornithologists Union in August in Chemnitz, Germany and at the Wader Study Group Conference in September in Cadiz, Spain.
- A contribution was made to a workshop in December in Denmark organised by Hans Meltofte on the implications of climate change on Arctic breeding shorebirds. An oral presentation was given and plans were made for several cooperative publications combining data from different arctic regions.

Year 2004

- A highlight in 2004 was the publication of the book "Shorebirds – An illustrated behavioural ecology", which deals extensively with the migrations of our arctic breeding shorebirds. The book was launched at the Global Flyways Conference in Edinburgh (which included ceremonial speeches from minister Veerman from LNV and his royal highness prince Charles) and each of the many hundreds of participants from all over the world received a free copy thanks to subsidies from WWF.
- In 2004 no expedition was carried out. All funds available were allocated to analysing and writing up the data collected during the field seasons of 2000-2002 at the Willem Barentz Biological Station near Dickson, Taimyr. In addition, we reviewed relevant literature to obtain estimates for parameters outside the breeding season that are important to our migration models. Our studies aim at identifying fitness consequences of arrival date and arrival condition, which provide a link between events occurring in the winter and migratory stopover areas of the birds, and their reproductive success. These consequences determine the shape of the 'terminal reward function' in the

mathematic models of bird migration, which in cooperation with the group of Prof. Klaassen at the NIOO-CL. We had several meetings and paid working visits to the NIOO.

- Progress was made with several publications for peer-reviewed scientific journals. Journal of Avian Biology accepted a paper for publication. Several manuscripts are nearing completion, so that they can be submitted for publication.
- Apart from the scientific papers, a popular scientific paper was written for the Dutch Bird Journal Limosa and was published in spring 2004.
- A working document, integrating the results of the three expeditions and describing how we arrived at various parameter estimates for the models was continually being updated. We ran simulations with provisional estimates for the two subspecies of Knot that depend on the Wadden Sea during part of the year, i.e. islandica and canutus.
- Oral presentations were given at the Global Flyways Conference in Edinburgh, a meeting on optimal migration in Denmark and a meeting of the Wader Study Group in Papenburg.
- A working visit was paid to Prof. Ydenberg, director of the centre for wildlife ecology in Vancouver.

Year 2005

- The year 2005 was mainly devoted to parameterizing the model, running simulations and performing sensitivity analyses. In this enterprise, Dr. Silke Bauer from the NIOO adapted the model and ran the simulations and the sensitivity analyses on the basis of input provided by Dr. Bruno Ens, Prof. Klaassen, Drs. Hans Schekkerman and Drs. Ingrid Tulp. In the course of the year, several working visits were paid to the NIOO-CL in Nieuwersluis.
- Oral presentations were given at the final conference on the ESF program on optimality in bird migration (migration in the life history of birds) in Wilhelmshafen in February 2005 and at the Wader Study Group meeting in Cork in early October 2005.
- The migration work was discussed at a special meeting organized by Prof. Willem Bouten of the University of Amsterdam on 20 June 2005.
- In the light of possibilities for continuation of the project, the results of the work were discussed with Dr. Hans Nieuwenhuis and Drs. Vincent van den Berk from the ministry of LNV. In addition, a new project proposal for the years 2006-2009 was developed in cooperation with Wetlands International.
- Based on the encouraging results of this project that the phenology of insect abundance may be predicted on the basis of meteorological data, a project proposal was formulated to extend this work to other parts of the arctic as part of the International Polar Year (see 0).
- Several manuscripts were finished and published.

Reports, papers and manuscripts

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Appendix 2 - Meteorological data

Table 9-1 lists monthly meteorological data for five different locations used by Wiersma & Piersma (1994) and Piersma (2002) to calculate the maintenance metabolic rate (MMR) and the daily existence energy (DEE) of Red Knots in these locations.

Table 9-1: Average monthly values of meteorological data for five different locations used by Knots. The last column is the DEE of the Knots calculated for those locations by Wiersma & Piersma (1994) and Piersma (2002). Area 1 is "De Kooy" in the Netherlands, which is representative of the Wadden Sea. Area 2 is Keflavik, which is representative of Iceland. Area 3 is Alert on Ellesmere Island, which is representative of arctic Canada. Area 4 is Dikson on Taimyr, which is representative of the Siberian tundra. Area 5 is the Banc d'Arguin in Mauritania. Data kindly offered by Popko Wiersma.

area	month	Temp (°C)	Wind (m/s)	Radiation (W/m ²)	DEE (W)
1	1	2.6	7.7	26	432
1	2	2.4	7.2	55	419
1	3	4.4	7.2	108	397
1	4	7.2	7.2	166	353
1	5	11.2	6.7	221	298
1	6	14.3	6.2	238	254
1	7	16.2	6.7	214	249
1	8	16.7	6.2	186	236
1	9	14.8	6.2	127	273
1	10	11.3	6.7	72	323
1	11	7.1	7.7	33	384
1	12	4.3	7.7	21	421
2	1	0.1	7.4	6	458
2	2	0.3	7.5	26	460
2	3	1.6	7.3	79	430
2	4	3.0	6.7	130	398
2	5	6.5	5.9	209	340
2	6	9.2	5.6	200	306
2	7	10.7	5.4	212	294
2	8	10.4	5.6	170	304
2	9	8.4	6.2	87	343
2	10	5.0	6.3	39	384
2	11	2.8	7.1	10	423
2	12	1.2	7.1	2	442
3	1	-31.9	2.2	0	600
3	2	-33.0	2.2	7	603
3	3	-32.9	2.0	136	575
3	4	-23.9	2.1	146	506
3	5	-11.3	2.2	271	384
3	6	-0.1	2.8	291	301
3	7	3.9	3.3	243	287
3	8	0.8	2.6	129	317
3	9	-9.5	2.7	60	419
3	10	-19.8	3.0	2	522
3	11	-24.8	2.5	0	554
3	12	-30.2	2.0	0	582

4	1	-27.5	8.4	0	718
4	2	-25.9	8.1	9	694
4	3	-25.0	7.4	62	661
4	4	-18.1	7.3	160	579
4	5	-8.2	7.1	231	554
4	6	-1.0	6.8	224	377
4	7	3.6	6.6	191	335
4	8	4.8	6.7	116	341
4	9	0.8	7.3	52	406
4	10	-7.2	8.1	16	504
4	11	-19.2	8.1	0	632
4	12	-24.3	8.0	0	680
5	1	18.3	6.4	259	216
5	2	18.7	7.3	287	216
5	3	19.1	8.3	369	215
5	4	19.4	8.9	387	213
5	5	19.9	9.5	423	210
5	6	21.0	9.3	441	198
5	7	23.0	8.5	459	171
5	8	24.0	8.4	441	160
5	9	23.0	7.7	369	175
5	10	22.6	7.1	332	176
5	11	21.0	6.0	266	193
5	12	18.5	6.3	253	219

Table 9-2 lists the mean monthly temperatures for sites visited by Knots. Average daily ambient temperatures were taken from the KNMI Climate Explorer for weather stations close the location of interest. For each location, between two and five weather stations had sufficiently long data series (at least covering the years 1960-1990) to be included. Data were averaged per month for the years 1960-1990.

Table 9-2: Mean monthly ambient temperature recorded in weather stations averaged for the years 1960-1990 near sites visited by Knots.

Station	long (N)	lat (E.)	jan	feb	mrt	apr	mei	jun	jul	aug	sep	okt	nov	dec
<i>N-Brittany</i>	49N	02W	5.6	5.47	6.74	8.18	11	13.6	15.5	15.7	14.3	11.8	8.37	6.62
<i>Wadden Sea</i>	53N	05E	2.1	2.3	4.6	7.5	11.7	14.7	16.3	16.4	14.0	10.5	6.2	3.3
<i>Morecambe Bay, Wash</i>	54N	02W	4.8	4.7	6.2	8.1	11.1	13.9	15.7	15.7	14.0	11.4	7.6	5.8
<i>Schleswig-Holstein</i>	54N	08E	0.8	1.2	3.7	7.1	11.8	15.1	16.5	16.4	13.7	9.9	5.3	2.1
<i>W Iceland</i>	65N	23W	-1.2	-0.7	-0.2	2.3	5.7	8.6	10.1	9.7	6.7	3.8	0.6	-1.0
<i>N Norway</i>	70N	22E	-5.5	-5.5	-3.6	-0.7	3.3	7.3	10.3	9.8	6.4	2.0	-2.0	-4.3
<i>Greenland/ Canada</i>	80N	70W	-30.8	-32.1	-30.9	-23.0	-9.8	0.4	4.2	2.2	-5.7	-16.1	-24.7	-28.5
<i>South Africa</i>	33S	18E	20.6	20.7	19.7	17.7	15.2	13.4	12.6	12.9	14.3	16.2	18.2	19.6
<i>Guinea-Bissau</i>	11N	16W	24.4	25.8	26.7	26.9	27.3	27.5	26.5	26.2	26.4	27.1	26.5	24.4
<i>Mauritania</i>	20N	17W	19.7	21.0	22.2	22.2	23.0	24.4	24.6	25.8	26.9	26.0	23.2	20.4
<i>Western France</i>	46N	02W	5.3	6.3	8.3	10.9	14.1	17.4	19.5	19.1	17.0	13.3	8.7	6.0
<i>White Sea</i>	65N	37E	-12.9	-11.3	-6.1	-0.5	5.7	11.7	15.1	13.0	8.2	2.1	-3.8	-9.0
<i>Taimyr Peninsula</i>	75N	89E	-29.7	-29.1	-25.5	-18.3	-8.8	1.8	7.8	6.3	1.0	-10.7	-22.3	-25.6

Appendix 3 - IPY proposal

The following expression of intent was submitted to the international organisation of the International Polar Year 2007-2008 (<http://www.ipy.org>). It received endorsement from the Dutch National Committee. The international JC (joint committee) filed it in the database with ID No 216 and assessed it formally as a proposal “that has potential to make a significant contribution to the IPY, but which could be further strengthened by collaboration and integration with other EoIs to better deliver the “intensive burst of internationally coordinated, interdisciplinary, scientific research and observations” that is the concept for IPY.” Subsequently, it was decided to incorporate our proposal in the full proposal “Arctic Wildlife Observatories Linking Vulnerable EcoSystems” headed by Gilles Gauthier. This full proposal had ID No. 11 in the IPY database and received a very positive endorsement from the international JC organising the International Polar Year.



Deadline for Submission - January 14, 2005
Email to jcel@bas.ac.uk or Fax to +44-1223-221270

1.0 PROPOSAL INFORMATION

1.1 Title of proposed activity

Predicting the effect of climate change on the migrations and reproductive success of arctic breeding waders
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1.2 Acronym or short form title of proposed activity

Climate change and arctic waders

1.3 Concise outline of proposed activity

Shorebirds (Charadrii) form an important part of the avifauna and thus the biodiversity of arctic (tundra) landscapes. Most of the species breeding in the circumpolar region are long-distance migrants wintering either in temperate or tropical coastal habitats both North and South of the equator, congregating on the way in spectacular numbers in areas like the Wadden Sea and Copper River Delta. Global climate change may affect these birds both in their winter and migration stopover sites (sea level rise, availability of intertidal habitats), during the migratory flights (wind conditions) and in the breeding range (climatic breeding conditions, vegetation belts). To understand and predict the consequences of climate change at the population level, the cumulative and interactive ramifications of these effects need to be studied. Over the past years, 'dynamic migration models' have been developed that achieve this (Weber et al. 1994, 1998, 1999, Clark & Butler 1999, Klaassen 2001).

A central point in the models is the relationship between arrival date and arrival condition on the one hand, and breeding success on the other (Ens et al. 1994). It is the interplay between this '*terminal reward function*' and (mortality) factors operating in the wintering grounds and along the migration routes that determines the optimal strategy and its associated reproductive output. Climate change will affect the outcome of the models by changing the properties of staging sites (e.g. rate of fuel deposition) or wind conditions en route (e.g. fuel loss during flight), while changes in the breeding areas may affect the terminal reward function itself (e.g. the optimal laying date).

Three years of fieldwork in Taimyr, Siberia (Schekkerman *et al.* 2003, 2004), yielded much information on the factors and constraints that shape this "terminal reward" function. Two seem to be of special importance: (1) survival of adult birds directly after arrival on the breeding grounds, when food resources are sometimes unavailable due to retarded onset of spring or cold spells, and (2) the timing of hatching of the chicks relative to the seasonal peak in availability of arthropod prey (Moltofte *et al.* MS, Tulp & Schekkerman MS). Peak dates of arthropod emergence turned out to be highly variable between years, depending on the temperature regime. Indeed, the effect of weather on arthropod activity is so strong that temperature records could be used to 'postdict' the seasonal patterns of insect availability from past temperature records some 30 years hence. These analyses indicated that birds appeared to time the hatch of their eggs to the 'average' food peak rather than changing their laying dates to account for yearly variation in food abundance. However, these analyses also showed that the timing of the food peak seems to have become earlier over the past decades, possibly causing a shift in the optimal laying date that may ultimately result in a conflict between factors (1) and (2) above (i.e., adult survival will have to be compromised to lay eggs to hatch with the new food peak).

There are indications that in Siberia, weather-driven variation in arthropod availability limits chick growth of shorebird chicks much more often than in some other parts of the Arctic, e.g. Greenland and the NE Canadian archipelago which seem to have a more dependable summer climate (Moltofte *et al.* MS). There is thus a clear interest in elucidating the interplay between weather variation, arthropod availability and chick growth in different parts of the circumpolar Arctic, to learn more about geographic variation in the terminal reward function. There are only few such places (N-Alaska, NE Greenland, NE-Canada, W-Taimyr, SE-Taimyr, Central-Taymir) where data is already available. We envisage a joint research program consisting of a multiple number of site-specific studies that include daily arthropod sampling to link availability to weather, and measuring breeding phenology and chick growth. We will take blood samples from all captured birds to obtain DNA. These sampling programs are then to be followed up by retrospective analyses of weather data to reveal long-term average patterns and changes. In addition, we will use DNA sequence information to infer historic population changes in relation to major climatic events further back in time. The final step in the enterprise is to incorporate this information in dynamic migration models of waders breeding in different areas and calculate the effect of climate change under different scenarios.

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1.4 Which IPY 2007-2008 theme(s) will be addressed by the project (see Note 1)

Theme 1 – The current state of the polar environment	Y
Theme 2 - Change in the polar regions	Y
Theme 3 - Polar-global linkages and interaction	Y
Theme 4 - Investigating new frontiers	N
Theme 5 -The polar regions as vantage points	Y
Theme 6 - Human societies in polar regions	N

1.5 What is the major target of the proposed activity (specify one – see Note 1)

Natural or social science research	Y
Education/Outreach and Communication	N
Data Management	N
Legacy	N
Other Targets	N

1.6 What significant advance(s) in relation to the IPY themes and targets can be anticipated from this project?

Theme 1: The Committee for Holarctic Shorebird Monitoring (CHASM) has identified the need to expand existing monitoring programs of arctic breeding waders to include environmental factors important for interpreting the trajectories of population trends, including physical and biological parameters, such as climate, habitat, predator and alternative prey variables. This study goes a long way to begin coordinating not only research teams but the type and quantity of data collected.
Theme 2: The project specifically aims to investigate the effect of climate change on the ecological synchrony and reproductive success of arctic breeding waders.
Theme 3: The dynamic migration models deal with the migrations of the waders spanning the entire globe. They can be used, once properly parameterized, to study the impact of climate change on each of the links in the migratory chain.
Theme 5: Because most avian population models indicate adult survival and reproductive success limit

population growth, collecting data on these factors are essential first steps to understanding recent documented declines in shorebirds. Studies in the Arctic offer an unusual vantage point with which to explore factors limiting population growth.

The prime target of this study is research in the natural sciences. However, the project will also contribute information on insect abundance to a decade-long database on the circumpolar breeding conditions of arctic birds <http://www.arcticbirds.ru/> with data on insect abundance. At present, the interactive website covers bird breeding success, rodent abundance (predation on wader nests is high in years of low lemming abundance) and climate. This site (or derivatives of the site) can also contribute to education and communication about the migrations of the arctic breeding waders.

1.7 What international collaboration is involved in this project? (see Note 2)

The international collaboration involves different research groups spread throughout the entire Arctic, studying climate, insect abundance and chick growth. Sites will include several that have an existing long-term record of climate (and sometimes also arthropod abundance) measurements and bird phenology data. The program will link with PRISM (Program for Regional and International Shorebird Monitoring) in the North American Arctic, and with work at Alert in northeastern Ellesmere Island, both of which have been proposed as IPY projects. In addition we will attempt to initiate studies in new locations; at the very least some sites where this type of investigation may be profitably executed will be explored.

In addition to the field work, several groups of international scientists will be involved in statistical analysis of the weather data, in genetic analysis, and in further development of the dynamic migration models.

2.0 FIELD ACTIVITY DETAILS

2.1 Outline the geographical location(s) for the proposed field work (see Note 3)

Locations for field work include:

- the Zackenberg Research Station on NE Greenland
- the field station at Medusa Bay on NW Taymir
- field station on SE Taymir
- study site in Central Taymir
- field stations in N-Alaska
- Alert on Ellesmere island in Canada

2.2 Define the approximate timeframe(s) for proposed field activities?

Arctic Fieldwork time frame(s)	Antarctic Fieldwork time frame(s)
06/2007 – 09/2007	mm/yy – mm/yy
06/2008 – 09/2008	mm/yy – mm/yy
06/2009 – 09/2009	mm/yy – mm/yy

2.3 What significant logistic support/facilities will be required for this project? Can these resources be usefully shared with other projects? (see Note 4)

Existing field stations and perhaps new field stations.
Helicopters and snow terrain vehicles for transport.

In many cases these facilities can be usefully shared with other projects.

2.4 Will the project leave a legacy of infrastructure? (see Note 1)

It is hoped that one or more new field stations may be established.

2.5 How is it envisaged that the required logistics will be secured? (one or more options can be identified)

Consortium of national polar operators	N
Own national polar operator	N
Another national polar operator	N
National agency	Y
Military support	Y
Commercial operator	Y
Own support	Y
Other sources of support	Y
Each group will secure its own logistics to reach their field station or study site. In some cases this will involve commercial operators of helicopters and in other cases military support. Funds will be supplied by national agencies.	

2.6 Has the project been "endorsed" at national or international level (see Note 5)

Y	The project fits nicely in the subjects for Dutch research for the International Polar Year identified by the Dutch IPY committee: what are the consequences of global climate change for "our" long-distance migrants? The project will also yield information on the demography of migratory birds on Greenland and Siberia. The Dutch IPY committee endorses the expression of intent. Endorsement is being sought from IPY committees in other countries.
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3.0 PROJECT MANAGEMENT AND STRUCTURE

3.1 Is the project a component (established over the IPY 2007-2008 timeframe) of an existing plan, programme or initiative or is it a new autonomous proposal?

New Project ?	Component of an existing or planned activity ?
It is primarily a new project, but it also builds on existing and planned activities. For instance, at the Zackenberg Research Station on NE Greenland, insects and climate have been monitored for the last ten years and it is intended to continue this monitoring in the future. At other sites, especially in North America, this represents an augmented effort over existing study protocols.	

3.2 How will the project be organised and managed? (see Note 6)

Each group is responsible for organising the field work at their field station. Before the field work starts one or more meetings will be organised to discuss field methods and decide on a basic protocol and data exchange. At these meetings it will also be decided which group or groups will do the statistical analyses and which group or groups will do the modelling. The genetic analysis will be made at the University of Oslo. Coordination will be shared between the groups.

3.3 What are the initial plans of the project for addressing the education, outreach and communication issues outlined in the Framework document? (see Note 7)

At present information on the breeding conditions of arctic birds is made available on the following web site <http://www.arcticbirds.ru/>. This web site is primarily directed towards fellow scientists. The first step is to include monitoring data on insect abundance on this web site. A possible next step would be to add pages that explain to a wider public the importance of the Arctic for the breeding waders and explain how these waders depend on coastal sites throughout the world for their survival during the nonbreeding season. The site might also explain how the birds make their migrations and how these migrations might be affected by climate change. Alternatively, a separate web site could be developed for this purpose. During the expeditions there might be regular contact with the media at home. Experience has taught us that the media are generally interested in covering these kinds of expeditions on a live basis.

3.4 What are the initial plans of the project to address data management issues (as outlined in the Framework document)? (see Note 8)

Data will be made available on a web site, if possible the breeding conditions web site already in existence <http://www.arcticbirds.ru/>. Data can be extracted from this web site on the following conditions. Data are provided with the intent that they are readily available for personal and public non-commercial use and may be reproduced, in part or in whole and by any means, without charge or further permission from the International Wader Study Group. However, proper reference to contributors of original data to the database must be provided in all cases, and due diligence should be exercised in ensuring the accuracy of the materials reproduced. Data are provided on an end-user basis - that is, data are provided to users, but are not to be passed on to third parties or otherwise redistributed.

3.5 How is it proposed to fund the project? (see Note 9)

Each group intends to obtain funds primarily from their own national granting agencies. Perhaps international funding agencies and private sources will also be approached.

3.6 Is there additional information you wish to provide?

The proposal is truly international and so many groups have already indicated their interest in the project that this space is used to give all the extra names, as the space under 4.2 does not suffice:

Name 7 Drs. Ingrid Tulp

Organisation Animal Sciences Group, WUR, Netherlands

Name 8 Dr. Liv Wennerberg

Organisation Natural History Museum, University of Oslo, Norway

Name 9 Dr. Michael Soloviev

Organisation Moscow State University, Russia

Name 10 Dr. R.I.G. Morrison

Organisation Canadian Wildlife Service, Canada

4.0 PROPOSER DETAILS

4.1 Lead Contact for the Expression of Intent

Title Dr.

First Name Bruno

Surname Ens

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4.2 List up to six other project members and their affiliation.

Name 1 Drs. Hans Schekkerman

Organisation Alterra-Texel, Netherlands

Name 2 Prof. Les Underhill

Organisation Avian Demography Unit, University of Cape Town, South Africa

Name 3 Dr. Marcel Klaassen

Organisation NIOO-CL, Netherlands

Name 4 Dr. Hans Meltote

Organisation NERI, Department of Arctic Environment, Denmark

Name 5 Dr. Richard Lanctot

Organisation Alaska Shorebird Coordinator, US Fish and Wildlife Service

Name 6 Prof. Ron Ydenberg

Organisation Director of Centre for Wildlife Ecology, Canada