Behavioral and energetic response of Arctic-breeding seabirds to environmental variability

Jorg Welcker

A dissertation for the degree of Philosophiae Doctor

UNIVERSITY OF TROMSØ
Faculty of Sciences
Department of Biology

NORWEGIAN POLAR
INSTITUTE
Research Department

March 2009

Behavioral and energetic response of Arctic-breeding seabirds to environmental variability

Jorg Welcker

A dissertation for the degree of Philosophiae Doctor

UNIVERSITY OF TROMSØ
Faculty of Sciences
Department of Biology

NORWEGIAN POLAR INSTITUTE
Research Department

March 2009

TABLE OF CONTENTS

PREFACE

This PhD study was funded by the Research Council of Norway through the ‘Marine ecosystem consequences of climate induced changes in water masses off West-Spitsbergen’ (MariClim) project. Supplemental funding was provided by the Norwegian Polar Institute, Svalbard Science Forum and the University of Tromsø.

This project has been a great experience for me, and I am indebted to many people who have made this work possible. First and foremost I would like to thank my main supervisor Geir W. Gabrielsen for introducing me to Svalbard and seabird energetics, for his great support, guidance and help throughout, for his encouragement whenever things went wrong and his unfailing positive attitude which made it a great pleasure to be his student. I also would like to thank Rolf A. Ims, my supervisor at the University of Tromsø, for being so reassuring in his advice, for always having an open door and for enduring my many emails with the subject line ‘stats question…’.

I have had the privilege to be part of two very active research networks, many members of which have become more than just colleagues in the past years. It was a pleasure to collaborate with the ‘little auk team’, Ann Harding (Ann, this thesis simply would have been impossible without you!), Nina Karnovsky, Harald Steen and Sasha Kitaysky, and I am very grateful for all their input, dedication and the many discussion we have had (unfortunately mostly via email) which were of invaluable help and inspiration to me. I equally enjoyed being part of the ‘kittiwake team’, and I would like to thank Børge Moe, Jannik Schultner, Claus Bech and Olivier Chastel for sharing their knowledge, for their constant support and all their valuable contributions to many aspects of my kittiwake work. Thank you all very much! I would also like to express my gratitude to collaborators and co-authors, especially John Speakman and Hallvard Strøm, who have contributed with constructive comments on my work.

Special thanks go out to all the people who helped me during my many months of field work. I am owing (big time) to Lotta Borg, Signe Christensen-Dalsgaard, Julia Delingat, Ansgar Diederichs, Ine Dorresteijn, Magnus Irgens, Kerstin Lye, Stefan Natterer, Jannik Schultner and Nina Seifert for their incredible energy and enthusiasm during our long working days in the field. Thank you for keeping up your spirits even after 15h of work and 5h of sleep and for climbing Mt Everest (twice!) to get to this noisy bunch of birds. Thank you for your friendship; you’ve been the best field team I can imagine. I am also very grateful to the staff of the Sverdrup Station at Ny-Ålesund for logistical support, especially Wojtek Moskal, who helped us out, and cheered us up, an uncountable amount of times.

I would like to thank all the people who have helped with laboratory work and sample analysis, especially Lotta Borg, Magdalene Langset, Børge Moe, Elin Noreen, Philip Riel, and John Speakman and his lab personnel, Paula Redman and Peter Thomson.

Many thanks also to the Norwegian Polar Institute for providing perfect conditions for a PhD student and to all my friends and colleagues at NP for the great time I had at the institute and our many absolutely non-scientific lunch conversations.

Finally, I would like to thank my family for all their support and encouragement; my parents for inspiring my interest in nature, Julia for all she means to me and Pia, who, with a smile, turns my world upside-down.

Tromsø, March 2009
Jorg Welcker

SUMMARY

Knowledge about the extent to which organisms inhabiting the Arctic are able to adjust to environmental variability is essential in order to predict the impact of future climate change. In this context, the flexibility of animals with respect to energy acquisition and expenditure may be of importance because energy is a fundamental resource required by all organisms to survive and reproduce. The aim of this thesis was to evaluate the flexibility of Arctic-breeding seabirds in foraging behavior and energy expenditure in response to environmental variability. Data on two focal species, the little auk *Alle alle*, a small alcid that breeds exclusively in high Arctic latitudes, and the kittiwake *Rissa tridactyla*, a medium sized gull species which is widely distributed in the northern Atlantic, were collected during the breeding seasons 2005-2008. In little auks, adjustment of foraging behavior to geographic variation in foraging conditions was examined by comparison of foraging trip durations and travel distances of birds breeding at five different locations across a large part of the species' global distribution. Temporal and gender differences in behavior in relation to prevailing conditions were determined by automated recording of foraging trip durations during two consecutive seasons at two breeding sites. The energetic response to environmental stochasticity was examined by comparing rates of energy expenditure during two contrasting seasons and variability over five years in little auks and kittiwakes, respectively. Measurements of energy expenditure were derived by the single-sample and two-sample doubly labeled water (DLW) method. To assess the potential impact of this method on the behavior of the study subjects and possible repercussions on resultant estimates of energy expenditure, behavioral observations were performed of kittiwakes subjected to the DLW procedure and non-treated control birds.

Comparison of foraging trip durations of parent little auks revealed that during chick-rearing this species adopts a bimodal foraging strategy in which they alternate single trips of long duration with several trips of short length, a strategy previously described for procellariiform seabirds. However, this stereotyped pattern was found to be highly flexible and adjusted to spatial and temporal variation in foraging conditions. Birds facing unfavorable conditions responded by increasing the duration of long foraging trips, during which birds predominantly feed for themselves, and by decreasing the frequency of short trips, where birds primarily collect food for the chicks. These modifications led to reduced chick feeding rates and lower reproductive success, indicating that behavioral adjustments did not allow birds to fully compensate for costs incurred by unfavorable conditions.

Furthermore, provisioning behavior of little auks was sex-specific, with increased duration of long trips in females leading to an overall male-biased chick feeding rate. These sexual differences were best explained by diverging energetic constraints of males and females, with females allocating more time to self-feeding during chick-rearing.

Adjustment and limitation of energy expenditure differed remarkably between the two study species. Metabolic rate in little auks was flexible and adjusted in response to variation in food availability. Birds increased energy expenditure when food was abundant. Elevated metabolism was associated with increased allocation to chick provisioning, resulting in enhanced chick survival, and increased allocation to self-maintenance, associated with a higher return rate of adults the subsequent season. In contrast, kittiwakes did not adjust their metabolic rate in response to environmental variability. In this species, metabolic rate was similar across all five study years despite large variation in foraging conditions. Instead, kittiwakes seemed to operate close to an energetic ceiling which seemed independent of extrinsic factors. In both species, individual variation in energy expenditure was not related to the probability of the parent birds to return to the colony the following season. Moreover, in little auks an increased return rate coincided with increased rates of energy expenditure. These results do not support earlier suggestions of a direct physiological cost in terms of increased mortality as a trade-off to elevated metabolism.

In addition this study demonstrates that the use of the DLW method may elicit behavioral modifications in the study subjects. Birds treated with the two-sample method were considerably less motivated to return to their nests after treatment, reduced their overall nest attendance, and presumably remained inactive for extended time periods while at sea. These behavioral modifications may lead to biased estimates of energy expenditure.

LIST OF PAPERS INCLUDED IN THE THESIS

I. Welcker, J., Harding, A. M. A., Karnovsky, N. J., Steen, H., Strøm, H. and Gabrielsen, G. W. (2009). Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle. Journal of Avian Biology*, in press (doi: 10.1111/j.1600-048X.2008.04620.x).

II. Welcker, J., Steen, H., Harding, A. M. A. and Gabrielsen, G. W. (2009). Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy. *Ibis*, in press (doi: 10.1111/j.1474-919X.2009.00931.x).

III. Welcker, J., Harding, A. M. A., Kitaysky, A. S., Speakman, J. R. and Gabrielsen, G. W. (2009). Daily energy expenditure increases in response to low nutritional stress in an Arctic-breeding seabird with no effect on mortality. *Functional Ecology*, in press (doi: 10.1111/j.1365-2435.2009.01585.x).

IV. Welcker, J., Moe, B., Bech, C., Schultner, J., Speakman, J. R. and Gabrielsen, G. W. (submitted). Evidence for an energetic ceiling in free-ranging kittiwakes *Rissa tridactyla. Journal of Animal Ecology.*

V. Schultner, J., Welcker, J., Nordøy, E. S., Speakman, J. R. and Gabrielsen, G. W. (manuscript). Application of the two-sample doubly labeled water method alters behavior and affects estimates of energy expenditure in the black-legged kittiwake.

1. INTRODUCTION

The Arctic is currently experiencing severe effects of global climate change. Major modifications of the physical environment, such as melting sea-ice, shrinking glaciers, and increasing air and ocean temperatures are likely to cause marked effects on Arctic ecosystems (IPCC 2007). These effects may be exacerbated due to the fact that low species diversity and relatively simple biological structure of polar areas are especially vulnerable to perturbations (e.g. McCann 2000). Predicting effects on Arctic biota is crucial because climate change is thought to be more intense in the Arctic than in any other region of the world (Clarke & Harris 2003, IPCC 2007). However, in order to predict the impact of future climate change, a clearer understanding of how and to what extent organisms inhabiting the Arctic are able to adjust to environmental variability is essential.

Marine apex predators are good model species to study ecological consequences of stochastic environmental fluctuations because they integrate and/or amplify effects on lower trophic levels of the food web. Seabirds are a particularly suitable study group as they constitute a major component of the Arctic marine ecosystem, and are relatively easy to study as they come to land to breed, often in large colonies. Seabirds are notable for their extreme life-history traits such as low fecundity, slow chick growth and long life expectancy (Lack 1968). Most seabirds lay only 1-3 eggs annually and chicks may take several months to be able to fly and leave the colony, or, in some cases, are continued to be fed at sea after fledging (Gaston & Jones 1998). Age of first breeding is often delayed and adult birds may live for several decades. These life-history traits are thought to have evolved in response to energetic constraints imposed by the scarce, patchy and unpredictable distribution of food resources in the marine environment (e.g. Ashmole 1971, Ricklefs 1990).

A central concept in life-history theory is that organisms have to allocate resources between competing traits such as reproduction, self-maintenance and growth in order to maximize lifetime reproductive success. A major resource in this context is energy. If adverse environmental conditions cause energetic limitations, allocation decisions are likely to be modified (see Fig. 1). In long-lived animals, allocation processes are predicted to prioritize self-maintenance over current reproduction because in these species fitness primarily depends on longevity, and even a small decrease in survival will have a large negative effect on lifetime reproductive success (Charlesworth 1980, Stearns 1992). Hence, fluctuations in resource availability are expected to mainly affect the breeding performance of seabirds, while future survival is thought to be altered only at high levels of energetic stress (Erikstad *et al.* 1998, Weimerskirch *et al.* 2001). However, the extent to which current reproductive output is impaired by food availability partly depends on the flexibility of the species with respect to energy acquisition and expenditure.

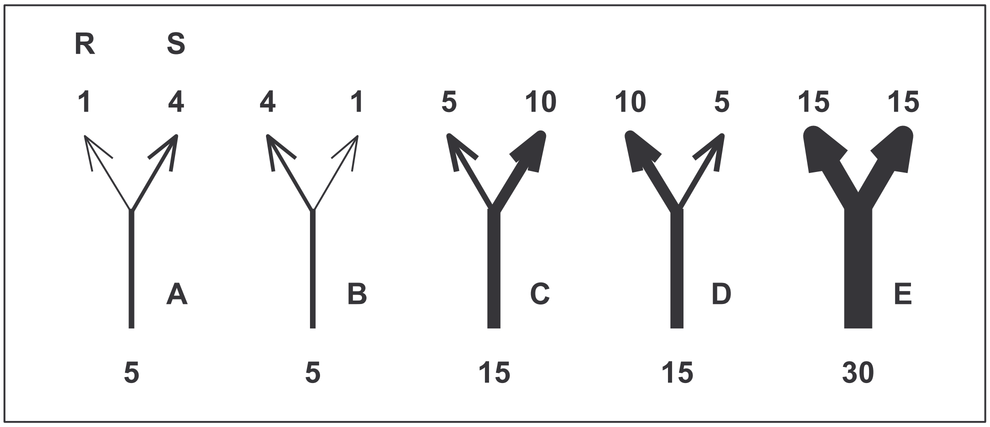

Fig. 1. 'Y-allocation' trees illustrating different resource allocation decisions (numbers at the tips of branches) for different amounts of resource input (number at the base). Maximum allocation to, or cost of, reproduction (R) and self-maintenance (S) is taken to be 15 resource units. Trees C and D illustrate a standard trade-off when the resource is limited. Trees A and B illustrate the aggravating effect of reduced resource availability. When resource input matches costs of both traits (tree E), no trade-off is incurred. After Zera & Harshman (2001).

1.1 Foraging behavior

Foraging determines an individuals' total energy budget and thus the amount of energy available to be allocated among competing fitness-related traits. Modification of foraging behavior in response to variation in food availability may buffer against environmental perturbations. Seabirds are central place foragers during the chick-rearing period (e.g. Ashmole 1971**),** frequently commuting long distances between foraging areas at sea and their breeding site on land. When resource availability close to the colony is limited, birds often rely on distant food sources to sustain breeding, and some seabird species have adopted a so-called bimodal foraging strategy (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1994). The bimodal foraging strategy involves the alternation of single trips of long duration (typically several days in most species) with single or several successive trips of short duration (typically one or few days; e.g. Weimerskirch 1998, Catard *et al.* 2000, Congdon *et al.* 2005). During short trips, birds are thought to forage primarily close to the breeding site to collect food for the offspring. However, short trips yield a negative energy balance to the parent birds and are conducted at the expense of body reserves. During long trips, birds are thought to utilize profitable foraging grounds at distance to the breeding site in order to replenish their depleted reserves (Weimerskirch 1998, Duriez *et al.* 2000). The decision whether to initiate a long or short foraging trip seems to be state dependent. Birds initiate a long trip when the proximity of a lower body mass threshold is reached, under which mortality risks due to starvation would be increased (Weimerskirch *et al.* 1999). The two trip types can therefore be regarded as the result of allocation decisions leading to alternating investment in reproduction (short trips) and self-maintenance (long trips).

Energetic costs of short trips are high, and birds catch a limited amount of prey during these trips (Weimerskirch *et al.* 2003). Although short trips increase the amount of energy delivered to offspring, parents are unable to perform only short trips because the foraging costs of these trips outweigh the energy gained. In contrast, long tips are energetically less expensive and, despite long travel distances, yield a high net rate of energy gain. However, performing exclusively long trips would result in a marked decrease in the amount of energy delivered to the offspring (Weimerskirch *et al.* 2003). Hence, a dual foraging strategy can be thought of as the optimal response to the trade-off between the need of the offspring to be fed frequently and that of the adults to forage efficiently in order to maintain energy balance. Bimodal foraging may therefore be an important strategy for maximizing fitness in species that rely on distant food sources (Weimerskirch 1998).

Energetic constraints due to low local resource availability and extended travel times to profitable foraging areas are usually considered to be the proximate causes underlying a bimodal foraging strategy. Considerable differences in travel distances between short and long trips have been documented in some species by satellite tracking (e.g. foraging ranges were 8 and 30 times larger during long compared to short trips in white-chinned petrels (Catard *et al.* 2000) and wandering albatrosses (Weimerskirch *et al.* 1997), respectively). For most species exhibiting bimodality in trips duration, however, foraging locations remain unknown. Recently, it has been suggested that a dual strategy may, under certain conditions, be profitable irrespective of foraging location. By modeling the optimal rate of prey ingestion by penguins, Ropert-Coudert *et al.* (2004) suggested that differences in stomach size between parents and offspring may result in two maximum rates of food gain: short trip durations may reflect the maximum rate of gain for chicks and the long trip lengths may represent the maximum rate of food gain for parents. By alternating short and long trips, parents would therefore maximize food gain for both themselves and their offspring irrespective of foraging location (Ropert-Coudert *et al.* 2004). Similarly, Congdon *et al.* (2005) suggested that dual foraging may be profitable even if birds always remained close to the colony because bimodal trip durations may help to minimize travel costs. However, these possibilities have not yet been tested.

The extent to which variation in food availability affects foraging decisions in bimodal foragers is not well studied. Some species may use a dual strategy as a facultative response to spatial and temporal variation in local foraging conditions (Granadeiro *et al.* 1998, Congdon *et al.* 2005). Birds may use a bimodal strategy when resource availability is poor and switch to a unimodal strategy when conditions allow. In other species, it has been shown that foraging behavior of dual foragers is adjusted by modification of the duration and frequency of the two trip types (Weimerskirch *et al.* 1999, Duriez *et al.* 2000).

There is mounting evidence that bimodal foraging is widespread among species of the order Procellariiformes (e.g. Weimerskirch *et al.* 1994, Weimerskirch 1998, Catard *et al.* 2000, Congdon *et al.* 2005). Outside this group, bimodality in foraging area or trip duration has been suggested for adelié penguins (*Pygoscelis adeliae*; Clarke *et al.* 1998) and brünnich's guillemot (*Uria lomvia*; Benvenuti *et al.* 1998). However, because bimodality in these cases may have resulted from a tendency of individuals to perform either long or short trips, the little auk *Alle alle* is the only non-procellariiform species for which a strategy of alternating short and long foraging trips has yet been described (Steen *et al.* 2007, paper I and II).

1.2 Energy expenditure

Energy is the most fundamental resource required by all organisms to survive and reproduce. The rate of energy expenditure integrates nearly all aspects of the ecology of a species, and reflects both the cost of living, i.e. the amount of energy an individual requires to maintain energy balance, and the amount of energy metabolized to be allocated to competing life-history traits. Factors limiting energy expenditure are therefore likely to be of paramount importance for the ecology of many animal species and may play an important role in the evolution of life-history traits and resource allocation strategies.

There are several pathways by which energetic limitation may be exerted. These may principally be divided into intrinsic constraints operating through physiological properties of the animals' body, and extrinsic constraints related to ecological factors that limit food availability or the capability/willingness of animals to obtain food from the environment. An intrinsic limitation may be centrally imposed by the capacity of the energy-supplying machinery, e.g. the maximum rate of the alimentary tract, the liver, kidneys or the heart to process, transport or excrete nutrients and wastes. Or it may be peripherally imposed by the energy-consuming machinery, i.e. the rate at which tissues can utilize the available energy (Weiner 1992, Hammond & Diamond 1997, Speakman & Krol 2005b). Although there can hardly be any doubt that physiological constraints ultimately limit the rate of energy expenditure, intensive laboratory research has not yet been able to establish the underlying mechanism(s) of this limitation (reviewed in Speakman 2008). Attempts to estimate the maximum sustainable rate of energy expenditure by means of inter-specific comparisons (Drent & Daan 1980, Peterson *et al.* 1990, Hammond & Diamond 1997) suggest that free-ranging species may usually operate well below their supposed physiological limit (Speakman 2000). However, this conclusion remains tentative because it is unknown to what extent the supposed ceilings can be generalized. In addition, there is a lack of experimental and empirical studies at the species level that explore whether intrinsic energetic limitation in free-ranging animals occurs or whether their rate of energy expenditure is usually limited by extrinsic factors.

Several proximate and ultimate explanations for an extrinsic limitation of energy expenditure have been offered (see Fig. 2). One key factor that is likely to have a strong impact on the rate at which individuals expend energy is food availability. Animals have to expend energy in order to obtain food, and the interplay between foraging success and foraging costs may determine the energy budget of an individual. Food availability may affect energy expenditure through two opposing processes: metabolic rate may be forced to increase by low resource abundance (forcing hypothesis) or enabled to increase by high levels of food supply (enabling hypothesis). The enabling hypothesis posits that individuals utilize the extra energy available during favorable conditions to increase their energy expenditure because the extra energy spent is associated with fitness benefits (Fig. 2; Speakman *et al.* 2003, paper III). Support for this hypothesis stems not only from studies reporting a positive relationship between metabolic rate and food availability for single species (Bryant & Tatner 1988, Speakman *et al.* 2003, Jodice *et al.* 2006a), but also from positive correlations between energy expenditure and the energy-richness of the diet or habitat among species (Speakman 2000, Mueller & Diamond 2001).

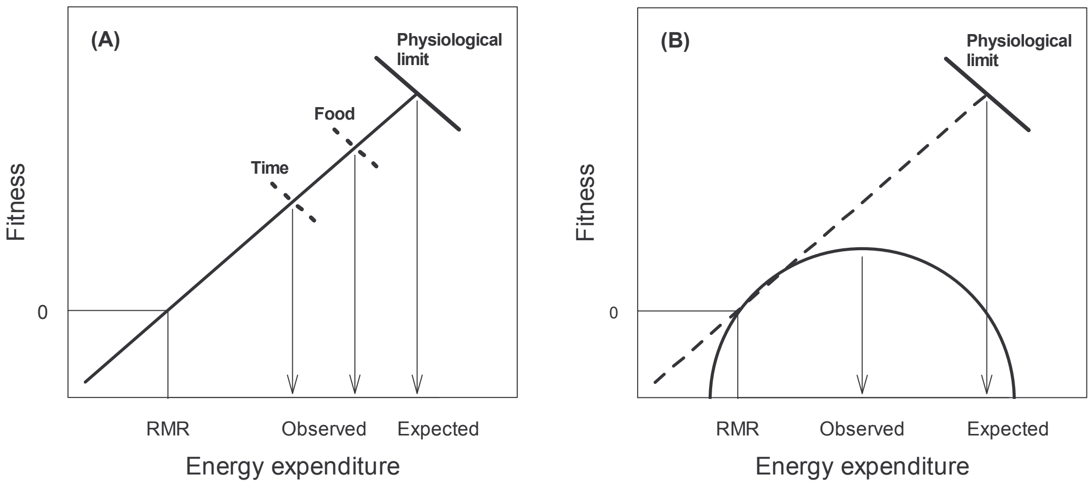

Fig. 2. Schematic diagram illustrating possible limitation pathways of energy expenditure. (A) Scenario without a fitness trade-off. Fitness increases with increasing expenditure until a physiological limit is reached. Constraints imposed by food supply or foraging time limitations may result in lower rates of energy expenditure than expected by physiological barriers. (B) Scenario with a fitness trade-off. Maximum fitness is achieved at a lower rate of energy expenditure than expected from the physiological model. Fitness trade-offs may be related to time allocation decisions, increased risk (predation, accident) or to a physiological cost leading to increased mortality (see text for details). Redrawn after Speakman (2000).

Conversely, the forcing hypothesis suggests that individuals raise their metabolism during unfavorable conditions by increasing their foraging effort in order to compensate for reduced food availability (Thomas *et al.* 2001, Speakman *et al.* 2003). This explanation implies that metabolic rate is not limited by the availability of food, but rather by fitness trade-offs associated with elevated metabolism and the willingness of individuals to increase foraging effort (Fig. 2). Everything else being equal, compensating behavior entails a runaway effect because the extra energy spent foraging must also be obtained and this therefore requires additional foraging and energy expenditure and so forth (Gorman *et al.* 1998). This positive feedback may make compensating behavior only feasible for small changes in food availability unless individuals are able to counterbalance the increased foraging costs, for example, by modifying body mass or resting metabolism, or reducing the allocation of energy to other functions such as immuno-competence or somatic repair (Wiersma & Verhulst 2005, Schubert *et al.* 2008).

Another important factor that may limit metabolic rate may be related to constraints on foraging time. Time may proximately limit energy acquisition and consequently expenditure if foraging is restricted by factors such as daylight length, tidal cycle, or prey behavior (Fig. 2). For example, Tinbergen & Verhulst (2000) argued that the energy expenditure of great tits *(Parus major*) may be proximately limited by daylight period, and birds may not be able to increase metabolic rate when demands increased because there was no more time available for foraging. However, time may also ultimately cause energetic limitation if an increased allocation of time to foraging resulted in a fitness trade-off, for example through compromised chick survival. This may especially apply to species where parents need to guard offspring to avoid high predation risk.

Alternatively, energy expenditure may ultimately be limited because an increase in metabolism may be associated with reduced future survival. Increased mortality may be brought about indirectly by an increased risk of predation or accident in connection with increased activity. More importantly, however, it has been suggested that mortality may increase with increased metabolism because of a deleterious physiological effect. This explanation is based on the rate of living/free radical damage hypothesis (Pearl 1928, Harman 1956, Beckman & Ames 1998). It suggests that increased metabolism leads to an elevated generation of free oxygen radicals, inevitable by-products of oxidative metabolism, which in turn may lead to increased somatic damage and consequently to accelerated aging and death. Although the free radical damage hypothesis and the relationship between metabolic rate and mortality have recently received great interest (see Hulbert *et al.* 2007, Monaghan *et al.* 2009 for reviews), few studies so far have explored this link in free-living species. Earlier studies, both experimental (e.g. Wolf & Schmid-Hempel 1989, Daan *et al.* 1996) and empirical (Bryant 1991), indicated a negative relationship between metabolic rate and survival, and lend support to the free radical damage hypothesis. However, recent evidence puts doubt on the supposed direct link between free radical production and metabolic rate (Brand 2000, Speakman *et al.* 2004, Selman *et al.* 2008a), undermining the central assumption of the free radical damage hypothesis. In addition, the effect of increased free radical production may also depend on the regulation of oxidative defense and repair mechanisms (reviewed in Monaghan *et al.* 2009). Elevated generation of free oxygen radicals may not lead to detrimental effects if counteracted by a corresponding increase in antioxidant and repair systems. Hence, whether or not metabolic rate is limited due to a physiological driven process affecting life span remains to be demonstrated.

As discussed, the regulation and limitation of energy expenditure may operate through several different processes, and the flexibility of the energetic response of animals to environmental variability may critically depend on these limiting factors.

1.3 Doubly labeled water method

All estimates of energy expenditure obtained in the course of this study were derived by the doubly labeled water (DLW) method. This is the most commonly used method to measure metabolic rate of animals in their natural environment (Butler *et al.* 2004). It is based on introducing heavy isotopes of hydrogen (either deuterium [^{2}H] or tritium [^{3}H]) and oxygen (^{18}O) into the body of the study animals, and estimating CO_2 production rate by comparing the elimination rates of both isotopes for a time period during which the animal ranges freely. The isotopes of oxygen and hydrogen can conveniently be administered as water (i.e. doubly labeled water) which quickly equilibrates with the body water of the subject. Subsequently, heavy hydrogen is washed out in water, e.g. as urine, in faces or by evaporation whereas ^{18}O is eliminated in water and CO_2 (see Fig. 3). Given that the size of the body water pool is known, a quantitative estimate of CO_2 production can be derived by the difference in elimination rates. The size of the body water pool can be calculated if the exact amount of isotopes introduced into the study animals is known and a sample is taken to estimate the initial enrichment of isotopes.

When applied in the field, the standard DLW method, also called the two-sample (TS) method, requires that the study animals are captured and bled twice. After initial capture, the animal is normally injected – intra-peritoneally or intra-muscularly – with the dosage of DLW and then held captive for a period of time, usually 0.5 to 2 h depending on the size of the animal, to allow for complete equilibration of isotopes with the body water. Then, an initial blood sample is taken and the animal is immediately released. Recapture is normally scheduled between 1 and 5 days post injection, upon which a second blood sample is taken in order to estimate final isotope enrichment.

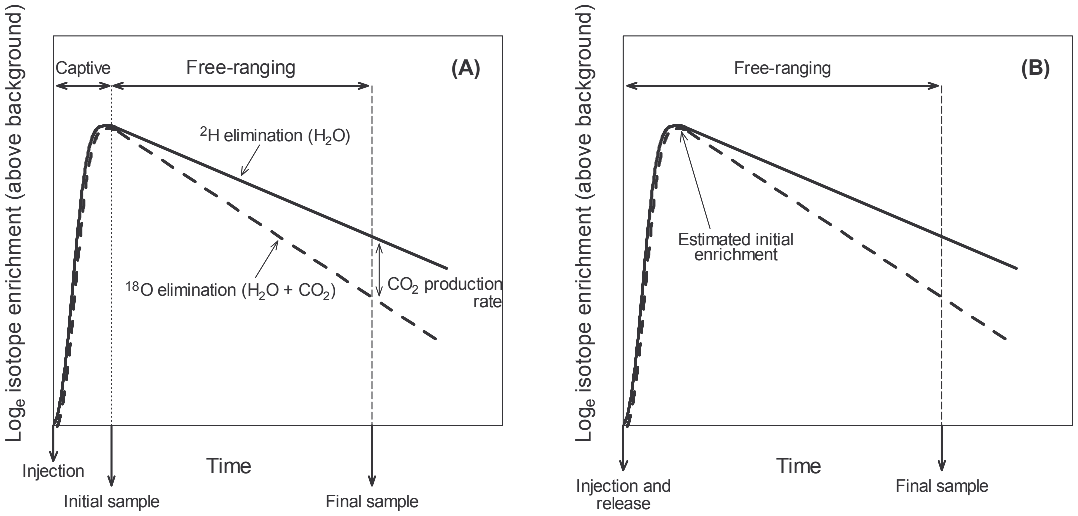

Fig. 3. Schematic diagram illustrating changes in isotopic enrichment of deuterium (^{2}H) and oxygen-18 (^{18}O) in the body of an animal following the injection of doubly labeled water (DLW). Isotopic enrichment increases steeply after injection until an equilibrium is reached. Subsequently, isotopes are exponentially eliminated from the body. Because ^{18}O is eliminated in both water and CO_2, its enrichment declines faster than that of ^{2}H. From the difference in isotope elimination rates a quantitative estimate of CO_2 production can be calculated.
(A) Two-sample DLW method. The study subject is restrained for the period of time it takes for isotopes to equilibrate with the body water. Following equilibration, an initial blood sample is taken to estimate isotope dilution space.
(B) Single-sample DLW method. The study subject is released immediately after injection and no initial blood sample is taken. Modified after Butler et al. (2004).

However, validity of the estimates of energy expenditure do not only depend on the precision and accuracy of the method itself, but also on the assumption that the behavior of the animals during the DLW measurement period reflects the natural behavior of these animals. Even though the DLW method is widely used in a large range of energetics studies in free-living animals this key assumption has rarely been tested systematically (reviewed in Speakman 1997). This is even more surprising because incidental evidence of adverse effects have been reported (e.g. Furness & Bryant 1996, Amat *et al.* 2000, Nilsson 2002), and an alternative, less invasive DLW sampling protocol, the so-called single or one-sample method, exists which has been suggested to mitigate potential effects (e.g. Amat *et al.* 2000, Jodice *et al.* 2003, Cresswell *et al.* 2004). The single-sample protocol is similar to the two-sample technique except that the study subject is released immediately after injection and therefore is not held captive for a prolonged time period and no initial sample is taken (Fig. 3; Webster & Weathers 1989, Speakman 1997). This approach requires an indirect estimate of initial body water pool size and equilibrium isotope enrichment. These estimates could be derived either from earlier studies that are likely to be comparable (paper III) or from a second group of animals from which an initial sample is taken according to the two-sample method (paper V).

There are several potential pathways by which the DLW method may affect behavior (Speakman 1997), the most important of which may be a stress response to the injection, restraint and bleeding procedure. More than 15 years ago, Speakman *et al.* (1991) found significant changes in the behavior of laboratory mice after they had been subjected to the two-sample DLW method and stated that studies on behavioral consequences in wild animals 'are urgently required' (Speakman *et al.* 1991). However, despite the large number of DLW studies published since then, no study dedicated to determine the potential effects on behavior and subsequent estimates of energy expenditure in free-living animals has been undertaken. The general conclusion that detrimental effects are negligible is largely based on peripheral information given in some publications (reviewed in Speakman 1997). There are several problems connected to this conclusion. Firstly, studies acknowledging detrimental effects greatly reduce their probability of getting published unless they are specifically aimed to assess the impact. Secondly, due to high financial costs and tedious and time-consuming field work, DLW studies often suffer from small sample sizes and consequently from low statistical power to detect effects. Finally, some studies have used techniques to detect effects that are themselves stressful (e.g. direct respirometry or radio-tracking; Zurowski & Brigham 1994, Speakman 1997). Hence, there is clearly the need for more vigorous testing of the behavioral effects of the DLW method, and studies that explore the potential of the single-sample method to assuage putative effects.

1.4 Study species

Two seabird species, the little auk (*Alle alle;* plate 1) and black-legged kittiwake (*Rissa tridactyla;* plate 1, hereafter referred to as 'kittiwake'), have been chosen for the purpose of this study. Both species are numerous in the Arctic, but due to their divergent foraging ecology, especially with respect to diet specialization, prey type (planktivorous vs. piscivorous) and foraging mode (diving vs. surface-feeding) may to differ in their response environmental variability.

Little auks are one of the smallest members of the family Alcidae, with an average body mass of about 160g (this study, Stempniewicz 2001). Their breeding range is concentrated in the high Arctic zone of the Atlantic, and, with an estimated population size of about 40 million breeding pairs (Harding *et al.* 2009a), it is among the most abundant seabirds in the world. Little auks feed almost exclusively on planktonic crustaceans (Pedersen & Falk 2001, Karnovsky *et al.* 2003), and are highly specialized on two species of *Calanus* copepods, *C. glacialis* and *C. hyperboreus*, that are associated with cold Arctic water masses (Scott *et al.* 2000, Beaugrand *et al.* 2002). Little auks establish their nest in crevices in scree slopes where they lay a single egg annually (Stempniewicz 2001). Both partners of a pair participate in incubation, brooding and chick provisioning. The chick is fed several times a day and parents bring food back to the colony in an extensible gular pouch. Parent birds adopt a bimodal foraging strategy during the chick-rearing period (Steen *et al.* 2007, paper I and II). The period of bi-parental care at the colony is followed by a period of male-only care at sea (Stempniewicz 2001). Females tend to cease chick feeding prior to fledging and the male parent accompanies the chick to sea (Harding *et al.* 2004). At that time, the chick weighs only about 70-80% of an adult bird but is fully capable of flying.

Plate 1. Black-legged kittiwake (*Rissa tridactyla*, left) and little auk (*Alle alle*, right) at their study sites in Kongsfjorden, Svalbard.

Little auks have a high field metabolic rate which, during reproduction, exceeds predictions based on body mass by more than 70% (Gabrielsen *et al.* 1991, Nagy *et al.* 1999). This is likely to be caused by high energetic costs of foraging and chick provisioning due to wing-propelled locomotion during diving, and the combination of energy intensive flapping flight, high wing loading and long foraging distances (Gabrielsen *et al.* 1991, paper

I). Due to their high rates of energy expenditure, it has been estimated that little auks have to consume about 80% of their body mass, or 60,000 prey items per day, in order to cover their own energy requirements (Gabrielsen *et al.* 1991, Harding *et al.* 2009a). The high energy expenditure and requirements of the little auk suggests that they may have little flexibility in their response to environmental variability and may therefore be especially vulnerable to long-term changes in the polar climate.

In contrast to the little auk, kittiwakes are widely distributed in the temperate and sub-arctic zone of both the Pacific and Atlantic and reaches its northern breeding range limit in the Arctic. The kittiwake is a medium-sized (body mass about 380g), cliff-breeding gull species which primarily feeds on small pelagic fish. The preferred prey species varies among breeding locations and includes polar cod (*Boreogadus saida*) and capelin (*Mallotus villosus*) on Svalbard and northern Norway (Mehlum & Gabrielsen 1993, Barrett 2007) and lesser sandeels (*Ammodytes marinus*) and pacific herring (*Clupea pallasi*) in Britain and the northern Pacific, respectively (Frederiksen *et al.* 2005, Jodice *et al.* 2006b). Kittiwakes usually lay 2-3 eggs, and both partners of a pair share parental duties throughout the chick-rearing period. Parent birds provision their offspring by regurgitating partly digested food at the nest site. In contrast to little auks, in which size difference between the two sexes is negligible (Jakubas & Wojczulanis 2007), kittiwakes are sexually size dimorphic with males weighing on average about 12% more than females (e.g. Angelier *et al.* 2007).

Earlier estimates of the field metabolic rate of kittiwakes closely correspond to that predicted by body mass (Gabrielsen *et al.* 1987, Nagy *et al.* 1999). Although kittiwakes only have to capture about 50% of their body mass of prey per day to cover their own energetic requirements (Piatt *et al.* 2007), the cost of rearing chicks increases their energy requirements substantially. Whereas little auk chicks receive only about 15% of the food gathered by parents (Gabrielsen *et al.* 1991), kittiwakes need to provide an additional 50 and 100% of their own needs for a brood of one or two chicks, respectively. It has therefore been suggested that kittiwakes have little buffer against stochastic fluctuations in prey availability (Piatt *et al.* 2007).

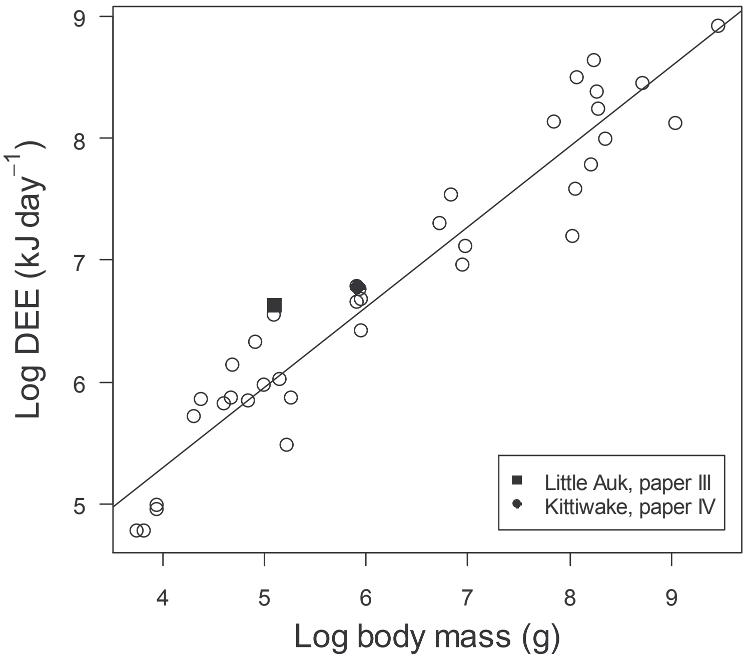

Fig. 4: Allometric relationship of daily energy expenditure (DEE) and body mass of 36 marine bird species. Mean metabolic rates of little auks and kittiwakes, as measured in the course of this study, are shown additionally. Data from Nagy *et al.* (1999) and references therein.

2. OBJECTIVES

The overall aim of this thesis was to evaluate consequences of environmental variability on the foraging behavior and energy expenditure of two key species of the Arctic avian community, the little auk and the kittiwake. Knowledge of their flexibility in these traits is important to detect the effects of future changes predicted in the Arctic marine environment. We evaluated the flexibility in the foraging behavior of little auks by determining the spatial, temporal and gender differences in behavior in relation to prevailing foraging conditions. The energetic response to environmental stochasticity was examined by comparing two contrasting seasons and variability over 5 years in little auks and kittiwakes, respectively.

The specific objectives were:

Paper I:

- To examine differences in foraging trip durations of little auks at 5 different breeding sites and assess how the bimodal foraging trip pattern is adjusted with respect to local foraging conditions.
- To determine the effect of travel distance from the breeding sites to the foraging areas on the duration and pattern of foraging trips.

Paper II:

- To determine whether foraging trip duration and provisioning behavior in little auks differs between males and females.
- To examine whether behavioral adjustments to temporal variation in conditions is dependent on the sex of the birds.

Paper III and IV:

- To assess the effect of fluctuations in food availability on the rate of energy expenditure in little auks and kittiwakes, and to determine fitness consequences in terms of chick fledging success and adult local survival associated with changes in energy expenditure.

Paper V:

- To determine potential effects of the single and two-sample DLW method used to estimate energy expenditure in paper III and IV, respectively, on the behavior of the study animals.
- To assess whether altered behavior affects estimates of metabolic rate derived by this method.

3. MATERIALS AND METHODS

3.1 Study area and data collection

This thesis is primarily based on field data collected in Kongsfjorden (78°54′N, 12°13′E), located at the west coast of Spitsbergen, Svalbard, Norway during the breeding seasons 2005 – 2008. The little auk study site was located at Feiringfjellet at the northern part of Kongsfjorden and comprised approximately 1,000 – 1,500 breeding pairs. Kittiwakes were studied at several small to medium-sized colonies in the inner part of the fjord consisting of a few dozen to several hundred pairs. The breeding period at Kongsfjorden is characterized by continuous daylight, an average ambient temperature of about +5ºC and relatively little precipitation occurring as either rain or snow.

Additional field work on the foraging ecology of little auks was conducted at four study sites located across a large part of the species' global distribution; namely at Kap Höegh (70º43′N, 21º38′W), East Greenland, on Bear Island (74º23′N, 19º01′E), and at Hornsund (77º00′N, 15º22′E) and Isfjorden (78º12′N, 15º20′E), both located at the west coast of Spitsbergen.

3.2 Foraging behavior

In order to compare the foraging behavior of little auks among study sites, direct observations of color-marked individuals were performed. Observations were scheduled to take place at the same breeding stage (mid chick-rearing period) to avoid any potential confounding effects of chick age. Activity data and estimated foraging ranges were derived by use of miniature temperature-depth recorders (TDRs – Cefas G5 storage tag, Cefas, Suffolk, UK) which were deployed at East Greenland, Hornsund and Kongsfjorden in 2007. The devices were programmed to record temperature and pressure (converted to dive depth) every five seconds, and visual inspection of the data allowed us to determine three main types of behavior: colony attendance, flight, and time on water. Maximum foraging ranges were estimated by dividing the sum of flight durations by two and multiplying by an estimated flight speed of 20 m s^{-1} (Pennycuick 1987, Elliott *et al.* 2004).

To continuously record durations of foraging trips throughout the chick-rearing period in 2006 and 2007 we used automated recording systems based on VHF radio transmitters and passive integrated transponder (PIT) tags in Kongsfjorden and Isfjorden, respectively. In Kongsfjorden, a total of 73 parent little auks were fitted with a radio transmitter, the presence or absence of which was permanently recorded by a stationary receiver placed at the base of the colony. The functionality of the system was verified by two reference transmitters that remained in the colony and by opportunistic observations of radio-marked birds. In Isfjorden, a tube-shaped recording device, consisting of a PIT tag antenna and a photo-electric switch was placed in the entrance of known nests, the adults of which were subcutaneously injected with a PIT tag. Each time one of these birds passed through the system, time and identification number was recorded. The direction of the movement in or out of the nest was determined by the time difference between the passage of antenna and switch.

Although both systems reliably recorded the behavior of the birds with minimum interference, they resulted in systematic differences in estimates of foraging trip duration. The system in Kongsfjorden recorded the presence of the birds in the colony both inside and outside the nest, whereas only time spent inside the nest was registered at Isfjorden. Hence, estimates of foraging trip durations derived by the two systems were not directly comparable and consequently data were analyzed separately.

3.3 Energy expenditure

The rate of energy expenditure of little auks and kittiwakes was estimated by the DLW method as described above. The single-sample approach was used in little auks because a pilot study conducted at the East Greenland study site in 2005 (Harding *et al.* 2009a) had raised concerns about very low recapture rates when using the two-sample method in this species. In kittiwakes, the two-sample method was used in all study years in order to make results comparable to estimates of metabolic rates obtained earlier at the same site (1997 and 1998; paper IV). Additionally, the single-sample method was applied on a subset of kittiwakes in 2006 and 2007 in order to compare the behavioral response of birds to the two-sample method (paper V). Initial enrichment of isotopes and dilution space in little auks was estimated based on the relationship of body water to body mass established by desiccation of carcasses in an earlier study on this species (Gabrielsen *et al.* 1991). For kittiwakes subjected to the single-sample method, we calculated initial isotope enrichment based on the regression of initial enrichment on body mass derived from individuals subject to the two-sample method.

In order to calculate rates of energy expenditure from the raw data, a number of assumptions had to be made regarding (i) the calculation of isotope dilution space (plateau vs. intercept method), (ii) physical isotopic fractionation effects, (iii) the isotope turn-over pool (single pool vs. two pool model), and (iv) the source of energy metabolized during the measurement period.

(i) There are two different ways to estimate initial isotope dilution space, the plateau and the intercept method (Speakman 1997). The intercept method calculates isotope dilution space by extrapolating the washout curves of isotopes back to the time of dosage (intercept), including equilibrium time. In contrast, the plateau method assumes the initial sample, when adequately timed, to directly reflect initial enrichment (Speakman 1997). Although the plateau method may theoretically be expected to underestimate initial enrichment and therefore overestimate dilution space, a number of studies comparing plateau dilution space estimates with desiccation of carcasses, generally found a very close correspondence (e.g. Williams & Nagy 1984, Tiebout & Nagy 1991). In addition, the intercept method critically depends on the assumption that isotope elimination rates during the equilibration period (i.e. in captivity) are consistent with elimination rates when individuals are free-ranging (Speakman & Krol 2005a). For our study animals, this is obviously incorrect and we therefore applied the plateau method to calculate initial dilution space.

(ii) Physical isotopic fractionation occurs because differences in the nuclear structure of the different isotopes result in differences in their tendencies to change phase from liquid to gas. This causes a problem for the DLW method because, due to fractionation, the isotopes leaving the body do not have the same isotopic composition as the material left behind. It has been shown that omitting to correct for fractionation effects can lead to an overestimation of energy expenditure of up to 15% (Tiebout & Nagy 1991). However, correcting for fractionation is difficult because its effect depends on several factors such as temperature, type of the fractionation process (i.e. kinetic or equilibrium), or the fraction of water loss which is subject to fractionation, all of which are practically impossible to measure directly. We followed the recommendation of Speakman (1997) who modified earlier correction factors of Lifson & McClintock (1966). Speakman (1997) assumed a fractionated water loss of 25% and calculated the fractionation factor by combining kinetic and equilibrium fractionation factors in a ratio of 3:1 at a temperature of 37ºC. Recent validation studies have shown that the resultant correction factor is appropriate (Visser & Schekkerman 1999).

(iii) Originally it was assumed that, when introduced into the body, both ^{18}O and ^{2}H, equilibrate within the same pool, the body water pool (Lifson & McClintock 1966). However, ^{2}H is also involved in other exchange reactions (e.g. with proteins) and can be irreversibly incorporated into lipids (Butler *et al.* 2004). Hydrogen dilution space estimates therefore usually exceed calculated oxygen dilution space by approx. 4%, suggesting that the elimination rates of the isotopes should be multiplied by their respective dilution spaces when calculating CO_2 production rates. However, in small animals (e.g. birds < 1000g, mammals < 5000g) the larger hydrogen pool size is approximately balanced by elimination of hydrogen due to irreversible reactions (Speakman 1987). Indeed, validation studies have demonstrated that the application of two-pool models consistently underestimated energy expenditure in small animals

(Visser *et al.* 2000, Speakman & Krol 2005a) and therefore the single-pool model was applied in this thesis.

(iv) An assumption has to be made regarding the source of energy that is metabolized during the DLW measurement period in order to convert rates of CO_2 production to estimates of energy expenditure. Because body mass changed little during the measurement period in both little auks and kittiwakes (mean: 1.0% ± 4.1 SD and 1.2% ± 4.1 SD, respectively), it was assumed that energy was mainly derived from catabolism of ingested food. Therefore, year-specific caloric equivalents were calculated based on fat and protein composition of the diet. Diet samples were collected each year during the DLW measurement period and either directly analyzed for fat and protein content (kittiwakes) or composition estimated from published literature (little auks).

When these assumptions are appropriately considered, the discrepancy between the DLW method and indirect calorimetry has been shown to be on average less than 3% (Speakman 1997, Butler *et al.* 2004).

3.4 Foraging conditions

Quantifying foraging conditions or food availability in seabirds is notoriously difficult because it is the result of a complex interplay between a multitude of variables such as the abundance, accessibility, patchiness and predictability of prey (e.g. Cairns 1987). Therefore indirect proxies, e.g. behavioral, physiological or diet-based indices, are often used as measures of foraging conditions. In little auks, differences in sea surface temperature (paper I) and plasma levels of the stress hormone corticosterone (CORT, paper III) were used to gauge variability in food availability between study sites and years, respectively. Ocean temperature is likely to determine the quality of little auk foraging areas, because the distribution and abundance of *Calanus* copepods, the main prey of little auks during chick-rearing, is closely linked to water temperature (Falk-Petersen 2007, Loeng & Drinkwater 2007). *Calanus* species associated with cold water (*C. glacialis* and *C. hyperboreus*) are higher in lipid and total energy content than species associated with warmer water masses (*C. finmarchicus*; Scott *et al.* 2000), and accordingly little auks prefer cold water masses as their foraging habitat (Weslawski *et al.* 1999, Karnovsky *et al.* 2003).

The secretion of CORT, used as a proxy for food availability in paper III, is induced by food restriction. A number of studies have demonstrated a negative co-variation between CORT levels and food availability (e.g. Pravosudov *et al.* 2001, Lynn *et al.* 2003, Kitaysky *et al.* 2007). Both baseline concentration and maximum levels of CORT[1] were used, reflecting short-term and long-term changes in food availability, respectively (Kitaysky *et al.* 2007). In order to assess foraging conditions in kittiwakes, we used three independent proxies, breeding success, foraging trip duration and diet composition, which have previously been demonstrated to vary with foraging conditions in this species (Frederiksen *et al.* 2005, Barrett 2007, Piatt *et al.* 2007).

4. FINDINGS AND DISCUSSION

4.1 Foraging behavior of little auks

Findings from paper I and II confirm the initial indication (Steen *et al.* 2007) that little auks generally adopt a bimodal foraging strategy during the chick-rearing period. A bimodal trip pattern was evident at all five study sites, covering a large part of the global range of the species and comprising contrasting oceanographic conditions (paper I); it was evident in different years with disparate foraging conditions and in both sexes from hatching to fledging (paper II). The bimodal strategy was found to be highly flexible and adjusted at three levels: (i) the duration of long trips, (ii) the frequency of short trips and (iii) the total time spent foraging. The length of long trips was negatively related to foraging conditions: trip duration was extended in years with unfavorable conditions (paper II) and increased with increasing sea surface temperature among sites (paper I). Inter-colony variation in long trip duration was remarkable, with birds in Kongsfjorden, the site with poorest conditions, spending on average 70% more time on a long trip than their conspecifics at East Greenland where foraging conditions were favorable (paper I). However, the response of little auks seemed to some degree to be dependent on the sex of the birds, with male trip durations more responsive to changes in foraging conditions than females (paper II).

In contrast, the duration of short trips did not vary between sites, years or sexes, indicating that short trip length was largely independent of foraging conditions. However, the frequency of short trips was flexible and inversely correlated with long trip duration (paper I). Hence, birds responded to deteriorating conditions not only by increasing long trip duration but also by reducing the number of short trips. These adjustments of the dual

---

[1] Baseline CORT samples are taken within three minutes of capture to ensure that samples are not affected by handling stress. Baseline CORT reflects nutrional status of birds shortly (days) before sampling. Maximum CORT is measured in response to a standardized stressor (handling and restraint), usually after approx. 30 min, and is thought to reflect food-related stress over longer time periods (weeks).

strategy resulted in a decrease in chick feeding frequency, and suggest that additional costs incurred during unfavorable conditions were at least partly shunted to the chicks. Although parent birds mitigated this effect by increasing their overall time allocation to foraging when conditions were poor, feeding rates were still up to 25% lower at Kongsfjorden compared to East Greenland. Even though data on chick growth and survival was not available for all study sites, this large difference in feeding rates is likely to have a strong impact on these traits (e.g. Hamer *et al.* 1991, Kitaysky *et al.* 2000).

Chick provisioning rate was male-biased throughout the chick-rearing period, with males feeding chicks on average 15% more often per day than females (paper II). This difference was attributable to sexual divergence in the duration and frequency of long and short trips, respectively. Sexual differences in foraging and provisioning behavior in seabirds have often been described in sexually size dimorphic species, and size-related mechanisms have usually been invoked as explanations for these differences. Causes of sexual divergence in these traits in monomorphic species are debated (e.g. Lewis *et al.* 2002, Peck & Congdon 2006). Increased duration of long but not of short foraging trips of female little auks indicates that females allocate more time to self-feeding than males. In turn, this suggests that differential energetic requirements at other breeding stages, presumably costs of egg production or unequal participation in incubation, may lead to different energetic constraints of the sexes during the chick-rearing period (paper II).

As indicated by the activity data derived from TDRs, the distance to foraging areas was an important determinant of the duration of long trips. Accordingly, mean maximum foraging range was more than three times larger in Kongsfjorden compared to East Greenland. Long travel distances (e.g. approx. 220 km in Kongsfjorden, paper I) were unexpected because of the high energetic costs of flight in little auks (Gabrielsen *et al.* 1991). Long commuting flights may therefore considerably reduce foraging efficiency in this species. Differences in long trip duration between sites were not only related to travel distance but also to differences in the amount of time spent in foraging areas once they were reached (paper I). This may be explained by the need of the birds to compensate for high travel costs by increasing their time spent foraging.

Surprisingly, findings from paper I suggest that the two main preconditions thought to trigger a bimodal foraging strategy in seabirds, poor near-shore food availability and long travel distances to profitable foraging areas, did not apply to the East Greenland site. Low sea surface temperature and high abundance of energy-rich *Calanus* species close to the colony suggest favorable foraging conditions at this site (paper I, N. Karnovsky & A.

Harding, unpublished data). Also, differences in mean flight duration between long and short trips were small and seemed insufficient to cause bimodal foraging at this site. This suggests that bimodal foraging may be independent of the location of foraging areas in little auks. Instead, dual foraging may help birds to reduce flight costs. Due to their high metabolic rate, little auks have to consume food equivalent to 80% of their body mass each day (Gabrielsen *et al.* 1991). Given the duration of time necessary for digestion, using a unimodal strategy would require birds to commute to the colony with large amounts of food ingested, thereby increasing flight costs (Harding *et al.* 2009b). Remaining longer time periods at sea, however, may enable birds to acquire, process, and excrete the amount of food needed for self-maintenance and consequently reduce costs of traveling to the colony (Congdon *et al.* 2005). The two explanations for bimodality of foraging trip durations are not mutually exclusive, and may both, as indicated in paper I, account for the observed behavior in little auks.

Overall, these findings demonstrate that little auks are highly flexible in their foraging behavior and able to adjust to a large range of foraging conditions. However, modification of foraging behavior did not allow birds to fully compensate for increased foraging costs incurred by deteriorating conditions. Behavioral adjustments were partly done at the expense of the offspring, as indicated by reduced chick feeding frequencies (paper I and II) and lower fledging success (paper II). However, the lower body mass and reduced local survival of parent little auks during unfavorable conditions suggests that despite their flexibility in foraging behavior, adult birds also incurred a cost (paper III). Long travel distances of birds facing high local sea surface temperatures corroborate earlier suggestions that little auks may be dependent on access to cold Arctic water masses and their associated energy-rich copepod species in order to reproduce successfully. If travel distances to these areas further increase, foraging may become inefficient, making it impossible for birds to refill reserves during long trips. This may have severe negative effects on breeding performance, adult survival, and, eventually, the population size of this species.

4.2 Energetic response to changing condition

The energetic response to variability in foraging conditions and food availability differed between the two focal species. While little auks increased their field metabolic rate when food was abundant (paper III), daily energy expenditure (DEE) of kittiwakes remained constant over five years of study in spite of large variation in foraging conditions (paper IV).

Foraging conditions for kittiwakes were highly variable among the five study years, as indicated by the three proxies used. High breeding success, a high proportion of fish in the diet and relatively short foraging trip durations suggest favorable foraging conditions in 2005 and 2007. These years were in sharp contrast with 2006, which was characterized by low breeding success, a low proportion of fish in the diet, and long foraging trip durations. However, the rate of energy expenditure of kittiwakes did not vary correspondingly (paper IV). DEE did not increase during favorable years which would be expected if energy expenditure was limited by food availability (enabling hypothesis, paper III). Also, there was no indication of an elevated rate of energy expenditure during poor years which would be indicative of increased foraging effort to compensate for poor resource abundance (forcing hypothesis).

In contrast, little auks showed a high inter-annual variability in energy expenditure, with DEE during a food-rich year exceeding DEE during a food-poor year by more than 25% (paper III). This increase in metabolic rate was likely to be related to an increase in provisioning behavior, evident in both chick feeding rate and meal size. Little auks attained an increase in chick feeding rates by reducing time allocation to long trips and increasing allocation to short trips (paper I and II). As it has earlier been demonstrated that the energetic costs of long trips are considerably lower than those of short trips (Weimerskirch *et al.* 2003), this difference in time allocation may proximately explain the increase in DEE in the food-rich year. Increased provisioning effort significantly enhanced the probability of chicks to fledge successfully. Hence, elevated metabolic rate was ultimately associated with short-term fitness benefits, results that support the enabling hypothesis as an explanation for modification of DEE in little auks (paper III).

In opposition to some earlier studies, no evidence was found for a direct cost of elevated DEE in terms of a reduced survival probability in either little auks or kittiwakes. In both species, local survival was not related to individual variation in DEE (paper III and IV). Furthermore, a high adult return rate in little auks coincided with a high mean rate of energy expenditure during the preceding breeding season (paper III). This suggests that DEE in these species is not limited by a life history penalty imposed by a negative effect on future survival. The findings of this thesis therefore do not support the rate-of-living theory (Pearl 1928) and the free radical damage hypothesis (Harman 1956, Beckman & Ames 1998) proposed as a proximate mechanism to explain a negative relationship between metabolic rate and survival. This may be explained by recent findings that question a direct link between metabolic rate and the production of free oxygen radicals (Brand 2000, Speakman

2005), a fundamental assumption of the free radical damage hypothesis. In accordance, several experimental studies have failed to establish a close link between metabolic rate, oxidative damage and mortality (Speakman *et al.* 2004, Selman *et al.* 2008a, Selman *et al.* 2008b). In line with these studies, the results of the present thesis do not suggest that elevated DEE inevitably leads to a reduction in survival driven by a direct physiological trade-off.

Hence, energy expenditure in little auks seemed to be extrinsically limited by availability of food rather than by a fitness cost connected to elevated DEE. Conversely, there was no evidence for an extrinsic limitation of metabolism in kittiwakes (paper IV). In this species, DEE was not only independent of foraging conditions but also did not vary with inter-annual differences in ambient temperature, brood size, or, when corrected for body mass, parental sex. This lack of variation with extrinsic factors seems to support the idea of an intrinsic limitation of DEE. However, because no data was available that would allow inference about proximate (central or peripheral) mechanisms causing a potential intrinsic limitation, this conclusion is tentative. Experimental studies, e.g. challenging kittiwakes to increase their DEE, are needed to further explore the possibility of intrinsic energetic limitation in free-living species.

It may be argued that an intrinsic metabolic ceiling does not necessarily imply that kittiwakes were incapable to energetically respond to extrinsic factors. The body mass of parent kittiwakes varied considerably between study years (paper IV). A reduction of body mass during chick-rearing in this species is associated with a disproportionate reduction of mass and metabolic intensity of internal organs (Langseth *et al.* 2000, Ronning *et al.* 2008), which can lead to a reduction in resting metabolic rate (Bech *et al.* 2002). A down-regulation of resting metabolism may therefore enable kittiwakes to allocate a flexible amount of energy to activity and thereby adjust their energy budget to extrinsic constraints.

These results demonstrate that the energetic response to environmental variability in Arctic-breeding seabirds differs remarkably between species. It also shows that flexibility in energy expenditure may not be deduced from deviations in the metabolic rate as predicted by body mass. Little auks, which exceed predicted DEE by more than 70%, were highly flexible in their energy budget while kittiwakes, the metabolic rate of which closely corresponds to predicted values, were not. Little auks utilized excess energy available in the environment to increase resource allocation to both current reproduction and self-maintenance. However, they also had an apparently limited capacity to buffer against unfavorable conditions. In contrast, kittiwakes seemed to operate close to an energetic ceiling and appeared unable to adjust DEE to environmental variability.

4.3 Behavioral effects of the DLW method

The behavioral response of birds subject to the single and two-sample DLW method was, for the first time, systematically recorded and compared to the behavior of unmanipulated control birds (paper V). This was done during two successive breeding seasons, 2006 and 2007, which differed considerably in foraging conditions for kittiwakes (paper IV). The results of this study suggest altered behavior of kittiwakes in response to the two-sample but not to the single-sample method. While nest attendance of single-sample birds, measured within 24 h after injection, did not deviate from controls, that of two-sample birds was reduced by almost 50%. Additionally, the time it took for treated individuals to return to their nest after injection was on average more than 20 times longer for two-sample compared to single-sample birds. This effect persisted to a lower degree after subsequent captures, even though treatment at these times did not differ between methods. This suggests that birds responded more strongly to a similar treatment because of carry-over effects based on earlier experience. Furthermore, the impact of the two-sample method differed between years. Kittiwakes were less affected by the two-sample procedure during a favorable year (2007) compared to an unfavorable year (2006), suggesting that stress imposed by the DLW protocol may to some extent be additive, and birds may tolerate stress to a larger degree when overall conditions are favorable.

The negative effect of the two-sample method was likely to be related to the birds being held captive for a time period after injection (1h) rather than to the injection itself. The dosage of DLW was administered by intra-muscular injection into the pectoral muscle, a method which has been suspected to cause discomfort when large amounts of DLW are applied (Wilson & Culik 1995). However, the lack of an effect of injection in single-sample birds compared to controls clearly suggests that aberrant behavior was not related to the dosing procedure.

Estimates of energy expenditure derived by the two-sample method were on average about 15% lower than those obtained by the single-sample method. This difference was likely to be caused by changes in behavior while birds were at sea. Whereas in single-sample birds there was a strong positive relationship between DEE and the amount of time birds spent at sea, this was not the case in two-sample birds. This indicates that two-sample individuals may not have been foraging while away from the colony to the same extent as single-sample birds did, but may have been inactive for extended time periods, possibly to recover from handling stress.

This study demonstrates that the general assumption made by most researches that application of the DLW method has little impact on the behavior of the study subjects may be fallacious. Clearly, behavioral effects have to be taken into account when applying the two-sample method. When feasible, the single-sample approach seems to be preferential, leading to DEE estimates that may more accurately reflect unbiased rates of energy expenditure. Even though this method requires an indirect estimation of body water pool size, potentially introducing additional error, validation studies have shown that deviation from indirect calorimetry is not increased in comparison to the two-sample method (Webster & Weathers 1989).

5. CONCLUSIONS AND FURTHER PERSPECTIVES

This thesis has provided new knowledge on the flexibility of foraging behavior and adjustment of energy expenditure in response to environmental variability in little auks and kittiwakes breeding in the Arctic. More specifically:

- This thesis has shown that little auks generally adopt a bimodal foraging strategy during chick-rearing. This strategy is highly flexible and adjusted to spatial and temporal variability in foraging conditions. However, behavioral adjustments did not allow birds to fully compensate for unfavorable conditions as indicated by lower chick feeding rate, reduced fledging success and lower adult return rate. The little auk is to date the only non-procellariiform species for which a dual strategy has been demonstrated. The pronounce differences in the general foraging ecology between alcids and procellariiform seabirds suggest that a bimodal strategy may be profitable for a larger range of species and foraging conditions than previously thought.
- The duration of long foraging trips was partly determined by the distance to foraging areas. Estimated maximum foraging distances varied substantially between study sites, and unexpectedly exceeded 200km at Kongsfjorden. Locating and characterizing these foraging areas may be important to predict the effect of future oceanographic changes in the Arctic on the foraging efficiency of little auks and subsequent consequences for breeding performance and population size in this species.

- This study has demonstrated sex-specific foraging and provisioning behavior in little auks. These sexual differences seemed to be best explained by diverging energetic constraints of males and females, with females allocating more time to self-feeding during the chick-rearing period. Further research on the physiological state of the sexes prior to and subsequent to chick-rearing is necessary to confirm this conclusion. Further exploration of proximate and functional causes of sex differences in energetic constraints may also lead to new insights regarding the development of female desertion and male-only care during the late chick-rearing period in this species.
- Adjustment and limitation of the rate of energy expenditure differed between the two focal species. Energy expenditure of little auks was adjusted in response to food availability with birds increasing their DEE when food was abundant. As predicted by the enabling hypothesis, elevated DEE was associated with fitness benefits in terms of enhance current reproductive success and increased local survival of adults. In contrast, kittiwakes did not respond to variation in foraging conditions by modification of energy expenditure. Instead, metabolic rate of kittiwakes was similar across five study years, among parents with different brood sizes, and between sexes, indicating that kittiwakes may be operating close to an intrinsic metabolic ceiling during a time of peak demands. However, experimental research challenging birds to increase their metabolic rate is necessary to verify the findings of this correlational study.
- Contrary to expectation from the rate of living/free radical damage hypothesis this thesis provides no evidence of a survival cost related to an elevated rate of energy expenditure. The probability of adult birds to return to the colony was independent of DEE in both species. These results are in accordance with recent studies which called into question a direct link between metabolic rate, free radical generation and mortality. However, due to limitations with respect to study design (correlational) and temporal scope, interpretation of the data has to be treated with caution. Direct measurements of oxidative damage and defense mechanisms are needed to fully evaluate potential physiological pathways mediating possible trade-offs of a high metabolic rate.
- Both species seemed to be unable to increase energetic effort to buffer consequences of poor foraging conditions. Together with their apparent dependence on cold water masses for profitable foraging, this may make the little auk vulnerable to predicted ocean warming in the Arctic. However, if these changes lead to a relaxation of the energetic limitation in kittiwakes, this species may be less affected by future climate change.

- Potential negative effects on the behavior of the study subjects have to be taken into account when applying the two-sample DLW method. Kittiwakes, a species previously thought to be relatively insensitive to capture and handling, responded to DLW procedures by a marked decrease of the motivation to return to the nest, decreased overall nest attendance and presumably by being inactive for extended time periods when at sea. These behavioral modifications may lead to biased estimates of energy expenditure. In comparison, birds did not respond negatively when the single-sample DLW approach was applied, which may be the preferential method in free-living species.

6. REFERENCES

Amat, J. A., Visser, G. H., Perez-Hurtado, A. & Arroyo, G. M. (2000) Brood desertion by female shorebirds: a test of the differential parental capacity hypothesis on Kentish plovers. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **267,** 2171-2176.

Angelier, F., Clement-Chastel, C., Gabrielsen, G. W. & Chastel, O. (2007) Corticosterone and time-activity Black-legged budget: An experiment with kittiwakes. *Hormones and Behavior,* **52,** 482-491.

Ashmole, N. P. (1971) Seabird ecology and the marine environment. *Avian Biology* (eds D. S. Farner & J. R. King), pp. 223-286. Academic Press, New York.

Barrett, R. T. (2007) Food web interactions in the southwestern Barents Sea: black-legged kittiwakes *Rissa tridactyla* respond negatively to an increase in herring Clupea harengus. *Marine Ecology-Progress Series,* **349,** 269-276.

Beaugrand, G., Ibanez, F., Lindley, J. A. & Reid, P. C. (2002) Diversity of calanoid copepods in the North Atlantic and adjacent seas: species associations and biogeography. *Marine Ecology-Progress Series,* **232,** 179-195.

Bech, C., Langseth, I., Moe, B., Fyhn, M. & Gabrielsen, G. W. (2002) The energy economy of the arctic-breeding Kittiwake (*Rissa tridactyla*): a review. *Comparative Biochemistry and Physiology a-Molecular & Integrative Physiology,* **133,** 765-770.

Beckman, K. B. & Ames, B. N. (1998) The free radical theory of aging matures. *Physiological Reviews,* **78,** 547-581.

Benvenuti, S., Bonadonna, F., Dall'Antonia, L. & Gudmundsson, G. A. (1998) Foraging flights of breeding thick-billed murres (*Uria lomvia*) as revealed by bird-borne direction recorders. *Auk,* **115,** 57-66.

Brand, M. D. (2000) Uncoupling to survive? The role of mitochondrial inefficiency in ageing. *Biological Aging - Euroconference on Molecular, Cellular and Tissue Gerontology*, pp. 811-820. Pergamon-Elsevier Science Ltd, Spa, Belgium.

Bryant, D. M. (1991) Constraints on energy expenditure by birds. *Acta XX Congressus Internationalis Ornithologici,* **IV,** 1989-2001.

Bryant, D. M. & Tatner, P. (1988) The costs of brood provisioning: Effects of brood size and food supply. *Acta XIX Congressus Internationalis Ornithologici,* **V,** 364-379.

Butler, P. J., Green, J. A., Boyd, I. L. & Speakman, J. R. (2004) Measuring metabolic rate in the field: the pros and cons of the doubly labelled water and heart rate methods. *Functional Ecology,* **18,** 168-183.

Cairns, D. K. (1987) Seabirds as indicators of marine food supplies. *Biological Oceanography,* **5,** 261-267.

Catard, A., Weimerskirch, H. & Cherel, Y. (2000) Exploitation of distant Antarctic waters and close shelf-break waters by White-chinned Petrels rearing chicks. *Marine Ecology-Progress Series,* **194,** 249-261.

Charlesworth, B. (1980) *The evolution of age-structured populations,* Cambridge University Press, Cambridge, UK.

Chaurand, T. & Weimerskirch, H. (1994) The regular alternation of short and long foraging trips in the Blue Petrel *Halobaena caerulea*: a previously undescribed strategy of food provsioning in a pelagic seabird. *Journal of Animal Ecology,* **63,** 275-282.

Clarke, A. & Harris, C. M. (2003) Polar marine ecosystems: major threats and future change. *Environmental Conservation,* **30,** 1-25.

Clarke, J., Manly, B., Kerry, K., Gardner, H., Franchi, E., Corsolini, S. & Focardi, S. (1998) Sex differences in Adelie penguin foraging strategies. *Polar Biology,* **20,** 248-258.

Congdon, B. C., Krockenberger, A. K. & Smithers, B. V. (2005) Dual-foraging and co-ordinated provisioning in a tropical Procellariiform, the Wedge-tailed Shearwater. *Marine Ecology-Progress Series,* **301,** 293-301.

Cresswell, W., Holt, S., Reid, J. M., Whitfield, D. P., Mellanby, R. J., Norton, D. & Waldron, S. (2004) The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behavioral Ecology,* **15,** 498-507.

Daan, S., Deerenberg, C. & Dijkstra, C. (1996) Increased daily work precipitates natural death in the kestrel. *Journal of Animal Ecology,* **65,** 539-544.

Drent, R. H. & Daan, S. (1980) The prudent parent - energetic adjustments in avian breeding. *Ardea,* **68,** 225-252.

Duriez, O., Weimerskirch, H. & Fritz, H. (2000) Regulation of chick provisioning in the thin-billed prion: an interannual comparison and manipulation of parents. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **78,** 1275-1283.

Elliott, K. H., Hewett, M., Kaiser, G. W. & Blake, R. W. (2004) Flight energetics of the marbled murrelet, *Brachyramphus marmoratus*. *Canadian Journal of Zoology-Revue Canadienne De Zoologie,* **82,** 644-652.

Erikstad, K. E., Fauchald, P., Tveraa, T. & Steen, H. (1998) On the cost of reproduction in long-lived birds: The influence of environmental variability. *Ecology,* **79,** 1781-1788.

Falk-Petersen, S., Pavlov, V., Timofeev, S., Sargent, J.R. (2007) Climate variability and possible effects on arctic food chains: The role of *Calanus*. *Arctic Alpine Ecosystems and People in a Changing Environment* (eds J. B. Ørbæk, R. Kallenborn, I. Tombre, E. N. Hegseth, S. Falk-Petersen & A. H. Hoel), pp. 147-166. Springer Verlag, Berlin.

Frederiksen, M., Wright, P. J., Harris, M. P., Mavor, R. A., Heubeck, M. & Wanless, S. (2005) Regional patterns of kittiwake *Rissa tridactyla* breeding success are related to variability in sandeel recruitment. *Marine Ecology-Progress Series,* **300,** 201-211.

Furness, R. W. & Bryant, D. M. (1996) Effect of wind on field metabolic rates of breeding Northern Fulmars. *Ecology,* **77,** 1181-1188.

Gabrielsen, G. W., Mehlum, F. & Nagy, K. A. (1987) Daily energy expenditure and energy utilization of free-ranging black-legged kittiwakes. *Condor,* **89,** 126-132.

Gabrielsen, G. W., Taylor, J. R. E., Konarzewski, M. & Mehlum, F. (1991) Field and laboratory metabolism and thermoregulation in Dovekies (*Alle alle*). *Auk,* **108,** 71-78.

Gaston, A. J. & Jones, I. L. (1998) *The auks: Alcidae,* Oxford University Press, Oxford.

Gorman, M. L., Mills, M. G., Raath, J. P. & Speakman, J. R. (1998) High hunting costs make African wild dogs vulnerable to kleptoparasitism by hyaenas. *Nature,* **391,** 479-481.

Granadeiro, J. P., Nunes, M., Silva, M. C. & Furness, R. W. (1998) Flexible foraging strategy of Cory's shearwater, *Calonectris diomedea*, during the chick-rearing period. *Animal Behaviour,* **56,** 1169-1176.

Hamer, K. C., Furness, R. W. & Caldow, R. W. G. (1991) The effects of changes in food availability on the breeding ecology of Great skuas *Catharacta skua* in Shetland. *Journal of Zoology,* **223,** 175-188.

Hammond, K. A. & Diamond, J. (1997) Maximal sustained energy budgets in humans and animals. *Nature,* **386,** 457-462.

Harding, A. M. A., Egevang, C., Walkusz, W., Merkel, F., Blanc, S. & Grémillet, D. (2009a) Estimating prey capture rates of a planktivorous seabird, the little auk (*Alle alle*), using diet, diving behaviour, and energy consumption. *Polar Biology*, doi: 10.1007/s00300-009-0581-x.

Harding, A. M. A., Kitaysky, A. S., Hall, M. E., Welcker, J., Karnovsky, N. J., Talbot, S. L., Hamer, K. C. & Grémillet, D. (2009b) Flexibility in the parental effort of an Arctic-breeding seabird. *Functional Ecology,* **23,** 348-358.

Harding, A. M. A., Van Pelt, T. I., Lifjeld, J. T. & Mehlum, F. (2004) Sex differences in Little Auk *Alle alle* parental care: transition from biparental to paternal-only care. *Ibis,* **146,** 642-651.

Harman, D. (1956) Aging: a theory based on free radical and radiation chemistry. *Journal of Gerontology,* **11,** 298-300.

Hulbert, A. J., Pamplona, R., Buffenstein, R. & Buttemer, W. A. (2007) Life and death: Metabolic rate, membrane composition, and life span of animals. *Physiological Reviews,* **87,** 1175-1213.

IPCC (2007) Climate change 2007. Forth Assessment synthesis report of the Intergovernmental Panel on Climate Change IPCC. Available from www.ipcc.ch.

Jakubas, D. & Wojczulanis, K. (2007) Predicting the sex of Dovekies by discriminant analysis. *Waterbirds,* **30,** 92-96.

Jodice, P. G. R., Roby, D. D., Suryan, R. M., Irons, D. B., Kaufman, A. M., Turco, K. R. & Visser, G. H. (2003) Variation in energy expenditure among black-legged kittiwakes: Effects of activity-specific metabolic rates and activity budgets. *Physiological and Biochemical Zoology,* **76,** 375-388.

Jodice, P. G. R., Roby, D. D., Suryan, R. M., Irons, D. B., Turco, K. R., Brown, E. D., Thedinga, J. F. & Visser, G. H. (2006a) Increased energy expenditure by a seabird in response to higher food abundance. *Marine Ecology-Progress Series,* **306,** 283-293.

Jodice, P. G. R., Roby, D. D., Turco, K. R., Suryan, R. M., Irons, D. B., Piatt, J. F., Shultz, M. T., Roseneau, D. G., Kettle, A. B. & Anthony, J. A. (2006b) Assessing the nutritional stress hypothesis: relative influence of diet quantity and quality on seabird productivity. *Marine Ecology-Progress Series,* **325,** 267-279.

Karnovsky, N. J., Kwasniewski, S., Weslawski, J. M., Walkusz, W. & Beszczynska-Moller, A. (2003) Foraging behavior of Little Auks in a heterogeneous environment. *Marine Ecology-Progress Series,* **253,** 289-303.

Kitaysky, A. S., Hunt, G. L., Flint, E. N., Rubega, M. A. & Decker, M. B. (2000) Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Marine Ecology-Progress Series,* **206,** 283-296.

Kitaysky, A. S., Piatt, J. F. & Wingfield, J. C. (2007) Stress hormones link food availability and population processes in seabirds. *Marine Ecology-Progress Series,* **352,** 245-258.

Lack, D. (1968) *Ecological adaptations for breeding in birds,* Methuen, London.

Langseth, I., Moe, B., Fyhn, M., Gabrielsen, G. W. & Bech, C. (2000) Flexibility of basal metabolic rate in arctic breeding kittiwakes (*Rissa tridactyla*). *Life in the cold* (eds G. Heldmaier & M. Klingenspor), pp. 471-477. Springer-Verlag, Heidelberg and New York.

Lewis, S., Benvenuti, S., Dall'Antonia, L., Griffiths, R., Money, L., Sherratt, T. N., Wanless, S. & Hamer, K. C. (2002) Sex-specific foraging behaviour in a monomorphic seabird. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **269,** 1687-1693.

Lifson, N. & McClintock, R. (1966) Theory of use of turnover rates of body water for measuring energy and material balance. *Journal of Theoretical Biology,* **12,** 46-74.

Loeng, H. & Drinkwater, K. (2007) An overview of the ecosystems of the Barents and Norwegian Seas and their response to climate variability. *Deep-Sea Research Part Ii-Topical Studies in Oceanography,* **54,** 2478-2500.

Lynn, S. E., Breuner, C. W. & Wingfield, J. C. (2003) Short-term fasting affects locomotor activity, corticosterone, and corticosterone binding globulin in a migratory songbird. *Hormones and Behavior,* **43,** 150-157.

McCann, K. S. (2000) The diversity-stability debate. *Nature,* **405,** 228-233.

Mehlum, F. & Gabrielsen, G. W. (1993) The diet of high-arctic seabirds in coastal and ice-covered, pelagic areas near the Svalbard archipelago. *Polar Research,* **12,** 1-20.

Monaghan, P., Metcalfe, N. B. & Torres, R. (2009) Oxidative stress as a mediator of life history trade-offs: mechanisms, measurements and interpretation. *Ecology Letters,* **12,** 75-92.

Mueller, P. & Diamond, J. (2001) Metabolic rate and environmental productivity: Well-provisioned animals evolved to run and idle fast. *Proceedings of the National Academy of Sciences of the United States of America,* **98,** 12550-12554.

Nagy, K. A., Girard, I. A. & Brown, T. K. (1999) Energetics of free-ranging mammals, reptiles, and birds. *Annual Review of Nutrition,* **19,** 247-277.

Nilsson, J. A. (2002) Metabolic consequences of hard work. *Proceedings of the Royal Society of London Series B-Biological Sciences,* **269,** 1735-1739.

Pearl, R. (1928) *The rate of living,* University of London Press, London, UK.

Peck, D. R. & Congdon, B. C. (2006) Sex-specific chick provisioning and diving behaviour in the Wedge-tailed Shearwater *Puffinus pacificus*. *Journal of Avian Biology,* **37,** 245-251.

Pedersen, C. E. & Falk, K. (2001) Chick diet of dovekies *Alle alle* in Northwest Greenland. *Polar Biology,* **24,** 53-58.

Pennycuick, C. J. (1987) Flight of auks (Alcidae) and other northern seabirds compared with southern procellariiformes - ornithodolite observations. *Journal of Experimental Biology,* **128,** 335-347.

Peterson, C. C., Nagy, K. A. & Diamond, J. (1990) Sustained metabolic scope. *Proceedings of the National Academy of Sciences of the United States of America,* **87,** 2324-2328.

Piatt, J. F., Harding, A. M. A., Shultz, M., Speckman, S. G., van Pelt, T. I., Drew, G. S. & Kettle, A. B. (2007) Seabirds as indicators of marine food supplies: Cairns revisited. *Marine Ecology-Progress Series,* **352,** 221-234.

Pravosudov, V. V., Kitaysky, A. S., Wingfield, J. C. & Clayton, N. S. (2001) Long-term unpredictable foraging conditions and physiological stress response in mountain chickadees (*Poecile gambeli*). *General and Comparative Endocrinology,* **123,** 324-331.

Ricklefs, R. E. (1990) Seabird life histories and the marine environment - some speculations. *Colonial Waterbirds,* **13,** 1-6.

Ronning, B., Moe, B., Chastel, O., Broggi, J., Langset, M. & Bech, C. (2008) Metabolic adjustments in breeding female kittiwakes (*Rissa tridactyla*) include changes in kidney metabolic intensity. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology,* **178,** 779-784.

Ropert-Coudert, Y., Wilson, R. P., Daunt, F. & Kato, A. (2004) Patterns of energy acquisition by a central place forager: benefits of alternating short and long foraging trips. *Behavioral Ecology,* **15,** 824-830.

Schubert, K. A., Vaanholt, L. M., Stavasius, F., Demas, G. E., Daan, S. & Visser, G. H. (2008) Female mice respond differently to costly foraging versus food restriction. *Journal of Experimental Biology,* **211,** 2214-2223.

Scott, C. L., Kwasniewski, S., Falk-Petersen, S. & Sargent, J. R. (2000) Lipids and life strategies of *Calanus finmarchicus*, *Calanus glacialis* and *Calanus hyperboreus* in late autumn, Kongsfjorden, Svalbard. *Polar Biology,* **23,** 510-516.

Selman, C., McLaren, J. S., Collins, A. R., Duthie, G. G. & Speakman, J. R. (2008a) The impact of experimentally elevated energy expenditure on oxidative stress and lifespan in the short-tailed field vole *Microtus agrestis*. *Proceedings of the Royal Society B-Biological Sciences,* **275,** 1907-1916.

Selman, C., McLaren, J. S., Mayer, C., Duncan, J. S., Collins, A. R., Duthie, G. G., Redman, P. & Speakman, J. R. (2008b) Lifelong alpha-tocopherol supplementation increases the median life span of C57BL/6 mice in the cold but has only minor effects on oxidative damage. *Rejuvenation Research,* **11,** 83-95.

Speakman, J. R. (1987) Calculation of CO_2 production in doubly-labeled water studies. *Journal of Theoretical Biology,* **126,** 101-104.

Speakman, J. R. (1997) *Doubly labelled water - theory and practice,* Chapman & Hall, London.

Speakman, J. R. (2000) The cost of living: Field metabolic rates of small mammals. *Advances in Ecological Research, Vol 30*, pp. 177-297. Academic Press Inc, San Diego.

Speakman, J. R. (2005) Body size, energy metabolism and lifespan. *Journal of Experimental Biology,* **208,** 1717-1730.

Speakman, J. R. (2008) The physiological costs of reproduction in small mammals. *Philosophical Transactions of the Royal Society B-Biological Sciences,* **363,** 375-398.

Speakman, J. R., Ergon, T., Cavanagh, R., Reid, K., Scantlebury, D. M. & Lambin, X. (2003) Resting and daily energy expenditures of free-living field voles are positively correlated but reflect extrinsic rather than intrinsic effects. *Proceedings of the National Academy of Sciences of the United States of America,* **100,** 14057-14062.

Speakman, J. R. & Krol, B. (2005a) Comparison of different approaches for the calculation of energy expenditure using doubly labeled water in a small mammal. *Physiological and Biochemical Zoology,* **78,** 650-667.

Speakman, J. R. & Krol, E. (2005b) Limits to sustained energy intake IX: a review of hypotheses. *Journal of Comparative Physiology B-Biochemical Systemic and Environmental Physiology,* **175,** 375-394.

Speakman, J. R., Racey, P. A. & Burnett, A. M. (1991) Metabolic and behavioral consequenses of the procedures of the doubly labeled water technique on white (MF1) mice. *Journal of Experimental Biology,* **157,** 123-132.

Speakman, J. R., Talbot, D. A., Selman, C., Snart, S., McLaren, J. S., Redman, P., Krol, E., Jackson, D. M., Johnson, M. S. & Brand, M. D. (2004) Uncoupled and surviving: individual mice with high metabolism have greater mitochondrial uncoupling and live longer. *Aging Cell,* **3,** 87-95.

Stearns, S. C. (1992) *The evolution of life histories,* Oxford University Press, Oxford.

Steen, H., Vogedes, D., Broms, F., Falk-Petersen, S. & Berge, J. (2007) Little Auks (*Alle alle*) breeding in a High Arctic fjord system: bimodal foraging strategies as a response to poor food quality? *Polar Research,* **26,** 118-125.

Stempniewicz, L. (2001) *BWP Update* (The Journal of the Birds of the Western Palearctic). *BWP update, vol.3*, pp. 175-201. Oxford University Press, Oxford.

Thomas, D. W., Blondel, J., Perret, P., Lambrechts, M. M. & Speakman, J. R. (2001) Energetic and fitness costs of mismatching resource supply and demand in seasonally breeding birds. *Science,* **291,** 2598-2600.

Tiebout, H. M. & Nagy, K. A. (1991) Validation of the doubly labeled water method (^{3}HH ^{18}O) for measuring water flux and CO_2 production in the tropical hummingbird *Amazilia saucerottei*. *Physiological Zoology,* **64,** 362-374.

Tinbergen, J. M. & Verhulst, S. (2000) A fixed energetic ceiling to parental effort in the great tit? *Journal of Animal Ecology,* **69,** 323-334.

Visser, G. H., Dekinga, A., Achterkamp, B. & Piersma, T. (2000) Ingested water equilibrates isotopically with the body water pool of a shorebird with unrivaled water fluxes. *American Journal of Physiology-Regulatory Integrative and Comparative Physiology,* **279,** R1795-R1804.

Visser, G. H. & Schekkerman, H. (1999) Validation of the doubly labeled water method in growing precocial birds: The importance of assumptions concerning evaporative water loss. *Physiological and Biochemical Zoology,* **72,** 740-749.

Webster, M. D. & Weathers, W. W. (1989) Validation of single-sample doubly labeled water method. *American Journal of Physiology,* **256,** R572-R576.

Weimerskirch, H. (1998) How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in Sooty Shearwaters. *Journal of Animal Ecology,* **67,** 99-109.

Weimerskirch, H., Ancel, A., Caloin, M., Zahariev, A., Spagiari, J., Kersten, M. & Chastel, O. (2003) Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology,* **72,** 500-508.

Weimerskirch, H., Chastel, O., Ackermann, L., Chaurand, T., Cuenotchaillet, F., Hindermeyer, X. & Judas, J. (1994) Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour,* **47,** 472-476.

Weimerskirch, H., Cherel, Y., CuenotChaillet, F. & Ridoux, V. (1997) Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology,* **78,** 2051-2063.

Weimerskirch, H., Fradet, G. & Cherel, Y. (1999) Natural and experimental changes in chick provisioning in a long-lived seabird, the Antarctic Prion. *Journal of Avian Biology,* **30,** 165-174.

Weimerskirch, H., Zimmermann, L. & Prince, P. A. (2001) Influence of environmental variability on breeding effort in a long-lived seabird, the yellow-nosed albatross. *Behavioral Ecology,* **12,** 22-30.

Weiner, J. (1992) Physiological limits to sustainable energy budgets in birds and mammals - ecological impliactions. *Trends in Ecology & Evolution,* **7,** 384-388.

Weslawski, J. M., Stempniewicz, L., Mehlum, F. & Kwasniewski, S. (1999) Summer feeding strategy of the little auk (*Alle alle*) from Bjørnøya, Barents Sea. *Polar Biology,* **21,** 129-134.

Wiersma, P. & Verhulst, S. (2005) Effects of intake rate on energy expenditure, somatic repair and reproduction of zebra finches. *Journal of Experimental Biology,* **208,** 4091-4098.

Williams, J. B. & Nagy, K. A. (1984) Daily energy expenditure of savannah sparrows - comparison of time-energy budget and doubly-labeled water estimates. *Auk,* **101,** 221-229.

Wilson, R. P. & Culik, B. M. (1995) Energy studies of free-living seabirds: Do injections of doubly-labeled water affect Gentoo Penguin behavior? *Journal of Field Ornithology,* **66,** 484-491.

Wolf, T. J. & Schmid-Hempel, P. (1989) Extra loads and foraging life-span in honeybee workers. *Journal of Animal Ecology,* **58,** 943-954.

Zera, A. J. & Harshman, L. G. (2001) The physiology of life history trade-offs in animals. *Annual Review of Ecology and Systematics,* **32,** 95-126.

Zurowski, K. L. & Brigham, R. M. (1994) Does use of doubly labeled water in metabolic studies alter activity levels of common poorwills. *Wilson Bulletin,* **106,** 412-415.

7. INDIVIDUAL PAPERS

PAPER I

Welcker J, Harding AMA, Karnovsky NJ, Steen H, Strøm H, Gabrielsen GW (2009)

Flexibility in the bimodal foraging strategy of a high Arctic alcid, the little auk *Alle alle*

Journal of Avian Biology, in press (doi: 10.1111/j.1600-048X.2008.04620.x).

PAPER II

Welcker J, Steen H, Harding AMA, Gabrielsen GW (2009)

Sex-specific provisioning behaviour in a monomorphic seabird with a bimodal foraging strategy.

Ibis, in press (doi: 10.1111/j.1474-919X.2009.00931.x).

PAPER III

Welcker J, Harding AMA, Kitaysky AS, Speakman JR, Gabrielsen GW (2009)

Daily energy expenditure increases in response to low nutritional stress in an Arctic-breeding seabird with no effect on mortality

Functional Ecology, in press (doi: 10.1111/j.1365-2435.2009.01585.x).

PAPER IV

Welcker J, Moe B, Bech C, Schultner J, Speakman JR, Gabrielsen GW (submitted)

Evidence for an energetic ceiling in free-ranging kittiwakes *Rissa tridactyla*

Journal of Animal Ecology

PAPER V

Schultner J, Welcker J, Speakman JR, Nordøy ES, Gabrielsen GW (manuscript)

Application of the two-sample doubly-labeled water method alters behavior and affects estimates of energy expenditure in black-legged kittiwakes

UNIVERSITY OF TROMSØ

ISBN 978-82-8236-008-1