Ecological, Physiological and Behavioural Response of the Little Auk *Alle alle* to Variable Trophic and Environmental Conditions in the Arctic

Dorota Kidawa

Large-scale climate changes observed over the last few decades are taking place the most rapidly and severely in the Arctic. Understanding the present and the long-lasting consequences of these changes upon living organisms on the individual, population and ecosystem level is one of the research priorities. Arctic seabirds, composing the pelagic food webs, are an essential element of the ecosystem. The little auk (*Alle alle*) is the most numerous Arctic seabird, feeding on zooplankton and transporting huge amounts of organic matter from sea to land, thus supporting functioning of the nutrient-deprived Arctic ecosystem. Large areas of ornithogenic tundra around little auk colonies constitute a high diversity of plant and animal communities. For those reasons, the little auk is considered a keystone species of the Arctic ecosystem.

Although Arctic seabirds are highly adapted to extreme environmental conditions, their energy balance could be affected by energy demanding periods of the life cycle (e.g. parental care, moulting, fledging in chicks etc.), as well as unpredictable perturbations, such as food shortages, adverse weather conditions, higher flight costs or decreased foraging ability. All of these factors may affect physiology, foraging strategy or breeding success of the little auk. Energy demands of little auk chicks and adults are very high in comparison to other seabirds and force them to focus on energy-rich calanoid copepods that are associated with cold Arctic waters, such as *Calanus glacialis*. The composition of zooplankton communities is closely linked to oceanographic conditions and the predicted shift towards a warmer climate scenario may have a negative impact on the little auks' time and energy budgets, chick feeding frequency, breeding success, and, as a result, its population number and range of distribution. As a consequence, we can expect that large areas of tundra around little auk colonies may disappear. This may lead to habitat fragmentation and a substantial decrease in number and diversity of plants and tundra-related birds and mammals.

For all those reasons, the overall objective of my work was to investigate the ecological, physiological and behavioural response of the little auk to the increased energetic demands associated with the unfavourable trophic and environmental conditions. In the first part of my study I examined a physiological reaction (excretion of stress hormone, corticosterone) of adult little auks and chicks in response to adverse weather conditions and

increased energetic demands associated with parental care, and intensive growth and fledging in chicks [1]. In the second and third part of my study I concentrated on the behavioural changes of adult little auks, i.e. foraging strategy and parental effort, and the consequences for growth and survival of their chicks, in response to the increased flight costs [2] and changes in quality and availability of food on their foraging grounds [3].

Glucocorticoids are one of the front-line hormones that participate in the control of whole body homeostasis and the organism's response to stress. Elevated corticosterone levels have been suggested as a reliable indicator of poor condition or health, thus, reflecting how an individual or population copes with their environment. However, blood hormone concentration can change within a short time window after the exposition to a noxious stimulus, such as presence of predator or a capture and handling procedure. Therefore, as an alternative to evaluating corticosterone level in blood samples, I proposed here a non-invasive method for measuring faecal corticosterone metabolites (FCM) in the excreted samples of the little auk. Moreover, the excreted FCM represents a cumulative secretion over a number of hours, providing a more integrated measure of recent corticosterone secretion. However, due to differences in metabolism, gut flora and food composition between different species, it is necessary to provide a successful physiological validation for each species before a method can be reliably applied. In order to perform the validation for the little auk I conducted an adrenocorticotropic hormone (ACTH) challenge test and established the most effective immunoassay and the time delay between increased plasma corticosterone levels and their reflection in the excreted FCM for little auks of both sexes and two age groups. Methods of measuring faecal glucocorticoids levels have been described for a few bird species so far. This is the first time, when this method was described and applied for the little auk, a keystone species for the ecosystem functioning, which is considered to be highly sensitive to the observed changes in climate and oceanography in the Arctic [1].

Furthermore, I have revealed that poor weather conditions, which occurred during the chick-rearing period did not trigger increased corticosterone excretion in adult little auks. Also, during the consecutive weeks of the chick-rearing period the corticosterone levels of adults appeared to be stable. Nonetheless, the observed differences in adults' FCM levels between two studied breeding colonies, characterized by different distances to the foraging grounds, probably reflect different foraging efforts of birds. In contrast to adult birds, the increase of precipitation coincided with elevated FCM level in chicks. It results probably from the increased heat loss due to water gathering at the bottom of the nest chamber. Additionally, a rapid growth of contour feathers impairs the insulation and the thermoregulation costs seem

to be high for developing chicks. Chicks with higher FCM levels had lower body mass and fledged later than chicks with lower FCM levels. The increase of FCM concentrations with the chicks' age, as well as the correlation of FCM levels with their body mass and fledging age, may suggest that corticosterone is a good indicator of chicks' body condition and plays an important role in the transition from a sedentary lifestyle to flying and foraging independently [1].

Life-history theory predicts that the partition of resources between survival and reproduction should be regulated so that to maximize the lifetime reproductive success of the individual. The trade-offs between the self-maintenance and parental effort may appear when food is limited. Under conditions of high temporal and spatial variability in marine food supplies, selection should favour a flexible foraging strategy and parental investment. Indeed, some seabird species are able to buffer food shortages by adjusting foraging behaviour and time allocation. However, species with specialised feeding habits or energy-demanding food search techniques have less flexibility and are more prone to breeding failures. I hypothesized that parent birds would prioritize their own energetic demands over chick provisioning when the costs of foraging and parental care become too high. I supposed that little auks adjust their energy budget to the varying conditions through changes in duration and frequency of foraging flights, and consequently, the number of chick feedings. As a result of reduction in parental care I expected slower growth and development of chicks, and also lower breeding success.

Nonetheless, the environmental changes are slow and difficult to predict, whereas the experimental conditions may allow assessing the birds' reactions to the unfavourable conditions in a short time frame. In the second part of the study I aimed to investigate changes in behaviour of parent little auks with artificially increased flight costs. I compared the time budget, foraging activity, chick provisioning, and consequently, growth and survival of chicks between adult birds equipped with loggers (experimental birds) and control birds. I analysed the activity of parent little auks on the basis of the data from temperature loggers (experimental birds) and the continuous 48 h observation of individually marked birds (control group). As a result of the increased flight costs and thereby foraging, birds significantly reduced the frequency of feeding their chicks and spent less time at sea per 24 hours. Moreover, experimental birds performed long foraging trips, considered as self-feeding trips, more frequently, and short foraging trips (performed mainly for chick provisioning) less frequently than control birds. The reduced chick provisioning of the experimental birds had detrimental effects on the body mass and fledging time of their chicks [2].

In the third part of my study I made use of the variable foraging ground quality, considering water temperature, salinity and zooplankton structure, in two little auk colonies on Spitsbergen located in different hydrographical regimes, Magdalenefjorden and Hornsund fjord, in two contrasting seasons, 2009 and 2010. Comparing the chick diet, chick feeding frequency, duration of foraging trips, body mass of adults and chicks, and chick survival in different trophic conditions allowed testing the above hypothesis in the natural conditions. Measurements and sampling were carried out simultaneously at sea (in the foraging grounds) and on land (in the colonies). In general, the little auks' foraging grounds in the vicinity of Hornsund colony, compared to the foraging grounds in the vicinity of Magdalenefjorden colony, had more Arctic characteristics and consequently a higher contribution of the preferred, energy-rich copepod species, *Calanus glacialis*, in relation to less energetically profitable *Calanus finmarchicus*. However, in Hornsund the impact of Atlantic-origin waters was greater in 2010 than in 2009, while in Magdalenefjorden the situation in the studied seasons was reversed. The study revealed that in both study areas, in the season with the stronger impact of Atlantic waters birds adopted a similar strategy – they increased the overall duration of their foraging trips and decreased the frequency of chick feeding. In consequence, chicks were delivered with lower daily energy value of food, what resulted in reduced chick survival. Moreover, in less favourable foraging conditions, the growth of chicks was slower. It has to be emphasized that changes in the foraging strategy of adult birds did not coincide with changes in their body mass corrected for body size (considered as a condition index). The results suggest also that colony-specific features (e.g. the presence/absence of remote but still available high-quality foraging grounds that can be utilized by birds when the trophic conditions in the vicinity of the colony deteriorate) may determine the birds' foraging strategy and ability to modify it. Therefore, this inter-annual and inter-colony comparison made in two contrasting seasons and in two colonies characterized by different hydrographical regimes delivers much more valuable information about the impact of oceanographic conditions on the little auks than a single inter-colony or an inter-annual comparison. Such a comprehensive study, comparing a large number of variables characterizing foraging ground quality, measured directly at sea, with the birds' foraging strategy, parental efforts, body condition and nestling survival was lacking so far [3].

Above studies, describing changes in the little auks' behaviour in response to artificially increased flight costs [2] and to inter-annual and inter-colony variations in trophic conditions [3] lead to similar conclusions. The observed changes in foraging strategy of adult little auks, without accompanying changes in their body mass [3], but with a lower body mass

and/or slower growth of their chicks [2,3] seems to support the hypothesis that under unfavourable conditions parent little auks safeguard their own energetic demands, probably in order to maximize their lifetime reproductive success.

Although, little auks display a range of behavioural plasticity that allows them to maintain a relatively high breeding success in face of oceanographic variability, low quality of foraging conditions experienced during the developmental stage may have long-lasting consequences for the future reproductive outcome and the overall population number. The results of my study provide a better understanding of the response of little auks to the increased energetic demands caused by unfavourable environmental and trophic conditions. This knowledge may be crucial for constructing reliable scenarios of the effects of changes in climate and oceanography taking place in the Arctic ecosystem.

References

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