Isotopic segregation between sympatric seabird species increases with nutritional stress

Christopher P. Barger* and Alexander S. Kitaysky

Department of Biology and Wildlife, Institute of Arctic Biology, University of Alaska Fairbanks, Fairbanks, AK 99775, USA
*Author for correspondence (cpbarger@ualaska.edu).

Dietary segregation is essential for the coexistence of closely related species of animals. However, little is known about how changes in availability of food resources might affect trophic interactions of wild animals breeding in sympathy. Here, we examined how interannual variations in relative food availability (as reflected in blood levels of stress hormone corticosterone, CORT) affect food partitioning (assessed via a comparison of stable isotope δ15N and δ13C ratios of blood) between the common murre (Uria aalge) and thick-billed murre (Uria lomvia), breeding on a single colony in the Bering Sea. During a 6-year study, CORT varied among years but not between species, whereas stable isotope ratios varied among years and between species. Isotopic distance between species increased with increasing CORT. These results indicate that, when food was not limiting, both species relied on similar food resources. As foraging conditions deteriorated, murres diverged in their diets. We conclude that the degree of dietary segregation between Uria spp. varies with changes in the availability of food and is greatest during food shortages.

Keywords: trophic segregation; food availability; seabirds; corticosterone; stable isotopes

1. INTRODUCTION

The ecological theory of segregation predicts that multiple species competing for a single resource cannot persist indefinitely [1] and diet segregation, either through habitat selection or resource partitioning, is essential for coexistence of morphologically similar species [2]. In seabirds, food partitioning has been proposed as one of the major mechanisms responsible for the coexistence of several taxa at a single colony [3,4]. Interannual fluctuations in prey available to seabirds are usually driven by changes in oceanography and might affect the magnitude of the diet segregation needed for two species to coexist. An overlap in diets might reflect a superabundance of food, while diet segregation might be needed to alleviate competition for limited food resources; however, empirical data are limited [5].

Previous studies have shown that blood concentrations of the adrenal hormone corticosterone (main avian glucocorticoid, CORT) are an effective proxy for monitoring relative prey availability in seabirds [6,7]. Body tissue signatures of stable isotopes (SIs) δ15N and δ13C ratios have been used to profile trophic niches of individual seabirds [8]. While δ15N reflects the trophic level of prey consumed, δ13C indicates the spatial origin of food resources [8]. Here, we combine these techniques to determine how diet segregation between two closely related species of seabirds varies with interannual changes in prey availability and oceanographic conditions. Common (Uria aalge) and thick-billed (Uria lomvia) murres are colonial seabirds that often breed sympatrically in Arctic and subarctic regions. Previous studies assessed murre diets during reproduction through observations of food delivered to chicks, but adult diets are relatively unstudied, but see Iverson et al. [9]. The segregation theory predicts that such species would always segregate their foraging when breeding in sympathy; however, the empirical evidence is equivocal: murres have shown strong dietary differences in some instances [10] and utilization of similar prey in others [11]. Causal factors contributing to these variations in food partitioning are currently unknown, but changes in food availability have been suggested as a potentially important mechanism [12]. Diet segregation between the species could reflect changes in availability of food such that when food resources are abundant murres overlap in their diets [10], but when food becomes limited foraging niches become segregated [11]. Here, we test the prediction that greater food partitioning (as reflected in more distant SI ratios) will be observed in years with low food availability, as reflected in elevated CORT levels.

This study provides novel insights concerning the importance of changes in food availability on diet segregation between closely related species that breed in sympatry. Common and thick-billed murres breeding on Bogoslof Island share breeding habitat and are similar in reproductive phenology and colony attendance patterns: one would expect to find large differences in their foraging ecology. This study shows that when food was limited (elevated CORT), murres displayed niche partitioning (increased isotopic distance) by feeding on different prey and/or using alternate foraging habitats. However, we found that diet segregation was not static, as interspecific differences in isotopic signatures were negligible when food was abundant and only increased when nutritional stress became elevated (figure 2a). The divergence into different foraging niches may allow murres to avoid interspecific competition for limited food resources and meet the demands of reproduction during sub-optimal conditions.

Previous studies have shown that seabirds respond to food limitations through an increase in CORT secretion [15]. We found that CORT levels changed in parallel in both murre species during the six breeding seasons indicating that they were similarly affected by interannual environmental changes. The similarity of the relationships between isotopic distance and CORT or SST suggests that food limitations were induced by the interannual change in oceanographic conditions. During food-limited ‘warm’ years with higher levels of CORT, common (but not thick-billed) murres generally had higher δ13C values and δ15N values, (increased isotopic distance) by feeding on different prey and/or using alternate foraging habitats. However, we found that diet segregation was not static, as interspecific differences in isotopic signatures were negligible when food was abundant and only increased when nutritional stress became elevated (figure 2a).

The divergence into different foraging niches may allow murres to avoid interspecific competition for limited food resources and meet the demands of reproduction during sub-optimal conditions.

Previous studies have shown that seabirds respond to food limitations through an increase in CORT secretion [15]. We found that CORT levels changed in parallel in both murre species during the six breeding seasons indicating that they were similarly affected by interannual environmental changes. The similarity of the relationships between isotopic distance and CORT or SST suggests that food limitations were induced by the interannual change in oceanographic conditions. During food-limited ‘warm’ years with higher levels of CORT, common (but not thick-billed) murres generally had higher δ13C values and δ15N values, (increased isotopic distance) by feeding on different prey and/or using alternate foraging habitats. However, we found that diet segregation was not static, as interspecific differences in isotopic signatures were negligible when food was abundant and only increased when nutritional stress became elevated (figure 2a).

The divergence into different foraging niches may allow murres to avoid interspecific competition for limited food resources and meet the demands of reproduction during sub-optimal conditions.
Dietary segregation and stress  C. P. Barger & A. S. Kitaysky

myctophids, according to prey SI in the vicinity of the colony) than thick-billed murres (figure 1). This is in accordance with previous direct observations of the diet composition in these species [10,11].

The isotopic distance between species was also driven by fluctuations in the common murre δ13C ratios during years with elevated nutritional stress (figure 1). Interestingly, we found that the δ13C ratios in thick-billed murres were generally low and remarkably constant across years, whereas common murres had larger variability between the years and their δ13C ratios were always higher. Perhaps diet segregation in these two species was largely owing to changes in common murre foraging habitat selection. The higher δ13C ratios of common murres in food-limited years suggest that this species could have foraged on prey located in the shelf region of the Aleutian Archipelago, which is influenced by inflow of waters from the central Gulf of Alaska and characterized by relatively high δ13C [18]. In contrast, thick-billed murres seemed to be continuously feeding in oceanic waters surrounding Bogoslof Island on prey relatively low in δ13C [19].

Examining food limitations in conjunction with the degree of isotopic segregation between two potentially competing species provides a better understanding of the changes that occur in their foraging ecology in response to environmental variability (figure 2). Results of this study suggest that interspecific diet partitioning is dynamic and might be indicative of the negative effects of warming environmental conditions on food resources available to seabirds breeding in the ocean basin regions of the Bering Sea (figure 2). Our approach to quantifying interspecific trophic interactions highlights the potential impact of warming climate on dietary niche overlap between species, which has implications for other bird species that share resources. Despite the apparent utility of this study, there are shortcomings that must be addressed in future research. During years with small interspecific isotopic distance, murres could have potentially foraged on different prey with similar SI ratios. Although the very low SI ratios of the age-0 pollock (figure 1) make them a likely main prey of both murres during some years (i.e. 2005), we obtained only SI of prey collected in 2009 and could not account for the temporal variability of SI of prey in other years. Whether diet segregation varies among life-history stages even during favourable foraging conditions also remains to be examined.

Samples were collected under required permits and IACUC approval

This research project was supported by the North Pacific Research Board (NPRB publication no. 320 and BEST-BSIERP Bering Sea Project publication no. 31) and Centre for Global Change (CIFAR). We thank Sergei Drovetski, Scott Hatch, Sara Iversen, Dean Kildaw, Taya Kitaysky, John Piatt, Mike Shultz, Alan Springer and Shiway Wang for their help in the field; Luke Whitman for preparing prey for SIA and Zhenya Kitaiskaia for conducting hormonal analyses. We thank Sarah Hopkins, Jorg Welcker, Robert Wilson, Rebecca Young and two anonymous reviews for comments on this manuscript.


