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, Irving 311, Fairbanks, AK 99775, USA

*Author for correspondence (cpbarger@alaska.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 glucocorticosteroid, 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 Imsen 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.

2. MATERIAL AND METHODS

Murre samples were collected on Bogoslof Island (53°55′38″N 168°02′04″W) in the southeastern Bering Sea during 15 July to 1 August in 1999, 2000, 2004–2005 and 2008–2009.

Productivity of the southeastern Bering Sea and Gulf of Alaska ecosystems is affected by interannual changes in oceanographic conditions such that colder conditions are usually associated with higher abundance of zooplankton [13 and references therein], which in turn might increase availability of prey to murres [14]. We used the annual mean May sea-surface temperature (SST) in the southeastern Bering Sea (available at www.beringclimate.noaa.gov) as a proxy for changes in environmental conditions. We focused on incubating adults to avoid the potential effects of chick requirements on parental foraging. Birds were captured at mixed colonies of murres with noose poles and a blood sample was collected from the brachial vein within 3 min to reflect baseline CORT levels [6,15]. Red blood cells (RBCs) and plasma were separated by centrifugation and stored at −20°C until further analysis. Plasma concentrations of CORT were determined as previously described [6,15]. Inter and intra-assay variability coefficients were less than 6 per cent and 2 per cent, respectively.

SIs (δ13C, δ15N) were analysed from RBC. The use of RBC is important for two reasons: (i) it reduces the possibility of interference from lipids (most are removed with plasma) and (ii) RBCs are continuously replaced and provide a proxy of recent diet composition [16]. To provide information on the isotopic scope of prey, we report SI ratios of the main potential prey species [9] collected in the proximity of the colony in 2009. SIs in RBC and lean whole body tissue of prey were determined as previously described [17]. Replicate measures of internal laboratory standards indicated measurement errors to be ±0.16‰ δ15N and ±0.13‰ δ13C in RBC and ±0.12‰ δ13C and ±0.06‰ δ15N in prey. All statistical analyses were performed with STATISTICA v. 10. We used three separate general-linear models to determine differences in baseline CORT, δ13C and δ15N between years and species. CORT data were log-transformed to meet assumptions for parametric statistical comparisons. To examine how changes in diet segregation correspond with changes in CORT and SST, we conducted correlation analyses between calculated isotopic distance based on Euclidean distances of mean δ13C and δ15N signatures between species for each year.


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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 environmental changes. The similarity of the relationships between isotopic distance and CORT or SST suggests that environmental changes were positively correlated with CORT levels of common (n = 6, r = 0.83, p = 0.043) and thick-billed (n = 6, r = 0.86, p = 0.030) murres (figure 2a). Isotopic distances between species were positively correlated with SST (n = 6, r = 0.898, p = 0.015; figure 2b).

4. DISCUSSION
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myctophids, according to prey SI in the vicinity of the colony (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.

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Figure 2. The relationships between interspecific isotopic distances. (a) Nutritional stress (logCORT, mean ± s.e.); CORT pooled for both species on annual basis. (b) May sea-surface temperature in the southeastern Bering Sea. Numbers next to symbols indicate year of collection.


