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Isotopic segregation between sympatric seabird species increases with nutritional stress

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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 sympatry. 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 $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ 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, murre 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) $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ ratios have been used to profile trophic niches of individual seabirds [8]. While $\delta^{15}\text{N}$ reflects the trophic level of prey consumed, $\delta^{13}\text{C}$ 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*) murre 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 sympatry; however, the empirical evidence is equivocal: murre 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 murre 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 murre [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 murre 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 ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$) 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 $\pm 0.16\%$ $\delta^{15}\text{N}$ and $\pm 0.13\%$ $\delta^{13}\text{C}$ in RBC, and $\pm 0.12\%$ $\delta^{15}\text{N}$ and $\pm 0.09\%$ $\delta^{13}\text{C}$ in prey.

All statistical analyses were performed with STATISTICA v. 10. We used three separate general-linear models to determine differences in baseline CORT, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ 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 $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures between species for each year

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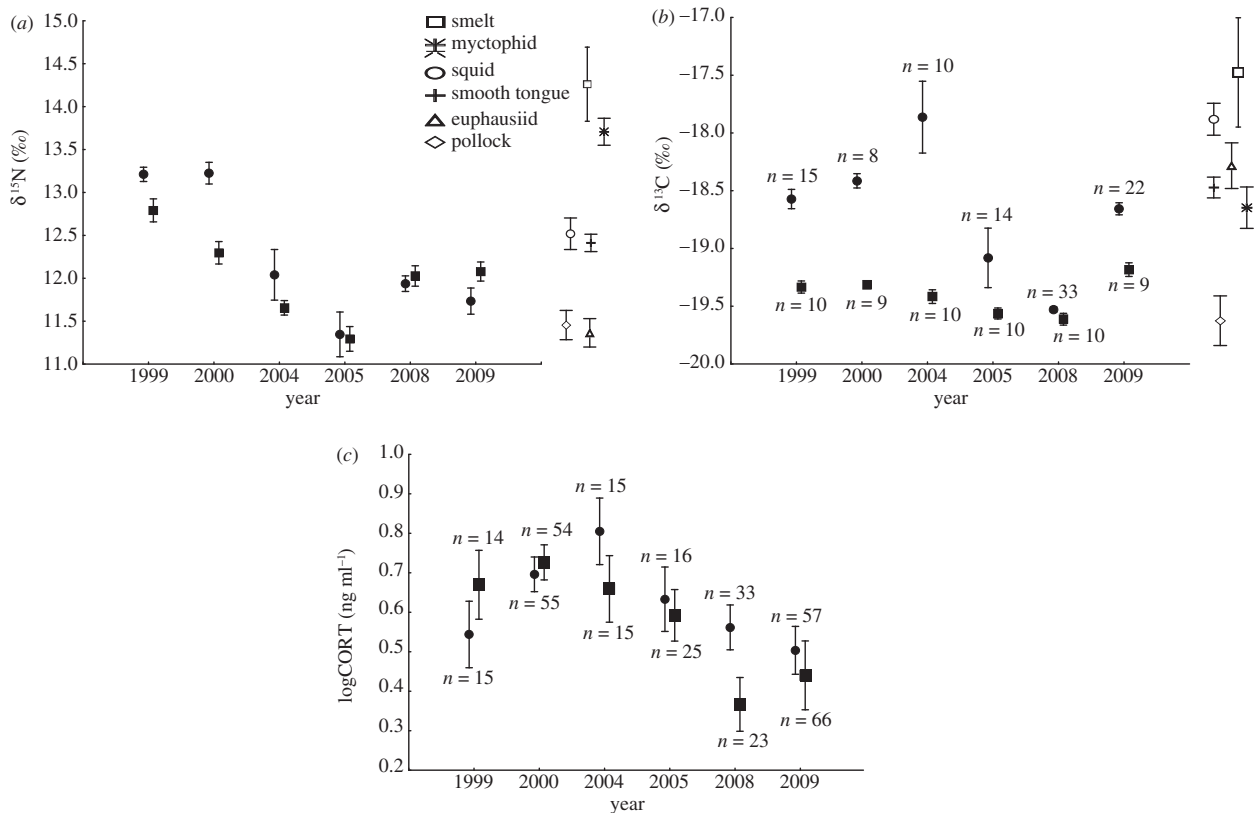


Figure 1. Interannual changes in stable isotope (SI) and CORT (mean \pm s.e.) of common (filled circles) and thick-billed murres (filled squares): (a) $\delta^{15}\text{N}$ values, (b) $\delta^{13}\text{C}$ values and (c) log baseline corticosterone. Sample sizes (n) are shown next to symbols (n were identical for $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$). SIs of the potential prey are reported to illustrate isotopic scope of the food web (assuming enrichment coefficients of 2.0‰ for $\delta^{15}\text{N}$ and 1.0‰ for $\delta^{13}\text{C}$).

(see electronic supplementary material, figure S1 for details), annual mean CORT for each species and SST. We also examined whether the species-specific variance in SI increased during the years with high CORT using Pearson's correlation analyses.

3. RESULTS

Baseline CORT levels were similar between species ($F_{1,296} = 1.33$, $p = 0.250$) but varied among years ($F_{5,296} = 6.44$, $p < 0.001$); interannual changes in CORT were parallel between species ($F_{5,296} = 1.41$, $p = 0.222$; figure 1). In contrast, SI ratios were different between species ($\delta^{13}\text{C}$: $F_{1,148} = 101.3$, $p < 0.001$; $\delta^{15}\text{N}$: $F_{1,148} = 5.26$, $p = 0.023$; figure 1) and years ($\delta^{13}\text{C}$: $F_{5,148} = 16.7$, $p < 0.001$; $\delta^{15}\text{N}$: $F_{5,148} = 26.73$, $p < 0.001$; figure 1); interannual changes were not in parallel between species ($\delta^{13}\text{C}$: $F_{5,148} = 8.3$, $p < 0.001$; $\delta^{15}\text{N}$: $F_{5,148} = 3.25$, $p = 0.008$). Interannual changes in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ variance did not correlate with changes in mean CORT in common and thick-billed murres (r -values < 0.63 , $n = 6$, associated p -values > 0.176). Isotopic distances between species 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

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 $\delta^{15}\text{N}$ ratios compared with food-rich 'cold' years. This suggests that during food-limited conditions common murres were using higher trophic level prey species (e.g. smelt and

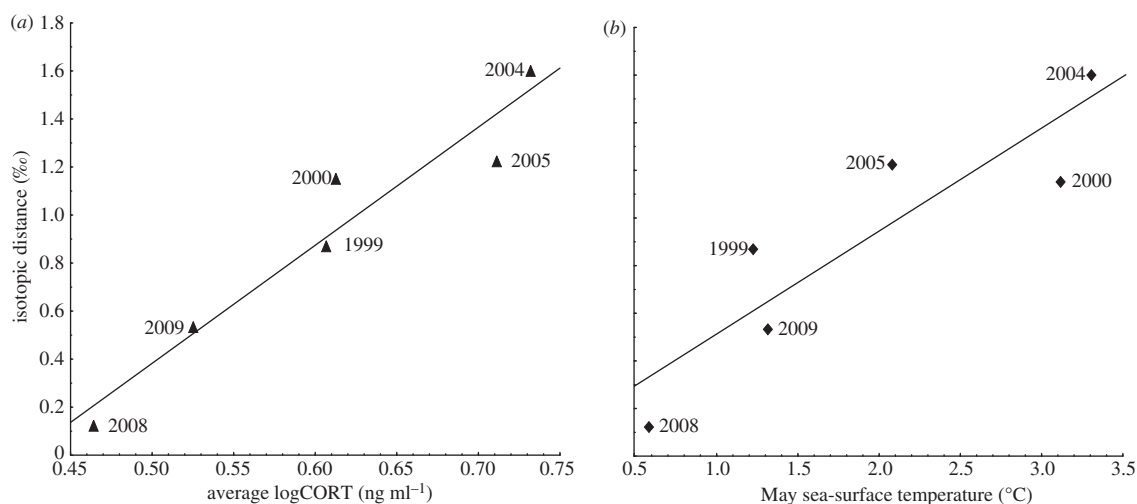


Figure 2. The relationships between interspecific isotopic distances. (a) Nutritional stress (logCORT, mean \pm s.e.); CORT pooled for both species on annual basis. (b) May sea-surface temperature in the southeastern Bering Sea. Numbers next to symbols indicate year of collection.

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 $\delta^{13}\text{C}$ ratios during years with elevated nutritional stress (figure 1). Interestingly, we found that the $\delta^{13}\text{C}$ ratios in thick-billed murres were generally low and remarkably constant across years, whereas common murres had larger variability between the years and their $\delta^{13}\text{C}$ ratios were always higher. Perhaps diet segregation in these two species was largely owing to changes in common murre foraging habitat selection. The higher $\delta^{13}\text{C}$ 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 $\delta^{13}\text{C}$ [18]. In contrast, thick-billed murres seemed to be continuously feeding in oceanic waters surrounding Bogoslof Island on prey relatively low in $\delta^{13}\text{C}$ [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

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