INTERNATIONAL JOURNAL OF PROGRESSIVE RESEARCH IN ENGINEERING MANAGEMENT AND SCIENCE (IJPREMS)

www.ijprems.com
editor@ijprems.com

Vol. 04, Issue 02, February 2024, pp : 28-32

e-ISSN : 2583-1062

Impact Factor : 5.725

THE IMPACT OF ENVIRONMENTAL ENRICHMENT ON FORAGING BEHAVIOR AND REPRODUCTIVE SUCCESS IN GENERALIST BIRD SPECIES

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ABSTRACT

Although competition is generally believed to encourage diversification within the same species' ecological niches, many species that appear to be generalists still display significant individual variations in their foraging specialization. This observation suggests that distinct cost-benefit considerations may underlie the diverse foraging specialization seen in individual members. While specialization can enhance foraging efficiency through a better understanding of the spatio-temporal availability of resources, it may also render individuals more susceptible to fluctuations in these resources.

This study utilized multiyear GPS tracking data from 19 Herring Gulls (Larus argentatus) breeding along the Belgian coast to examine potential variations in foraging effort and reproductive success based on different levels of foraging specialization. Initially, we measured spatial and habitat specialization during both incubation and chick-rearing phases across 31 individual breeding cycles, during which birds raised their young until reaching 21 days of age. Subsequently, we investigated the relationship between spatial and habitat specialization and two key indicators: daily distance covered (as a proxy for foraging effort) and chick growth (as a proxy for reproductive success).

Our findings revealed that the primary variation among birds was in their degree of habitat specialization. Habitat specialization correlated with decreased daily distances covered and increased growth rates of offspring, especially the youngest chicks. However, the positive effects of habitat specialization on chick growth diminished at high levels of spatial specialization. Consequently, our results demonstrate the fitness benefits of foraging specialization over our 5-year study period while underscoring the importance of longer-term studies, as environmental changes may cause these benefits to fluctuate throughout an individual's lifetime.

1. INTRODUCTION

In nature, intraspecific niche variation is a common phenomenon (Bolnick et al. 2003; Araújo et al. 2011), and many species labeled as generalist feeders actually comprise specialized individuals (Devictor et al. 2010). This has sparked significant interest among ecologists in unraveling the adaptive significance of individual foraging specialization and, consequently, the structure of individual niches within the broader population niche (Bolnick et al. 2007; Bolnick and Stutz 2017; Ingram et al. 2018; Sheppard et al. 2018).

The act of foraging specialization serves to diminish niche overlap and resource competition among individuals, thereby enhancing the adaptive value of specialized foraging strategies in the face of heightened intraspecific competition (Bolnick 2001; Svanbäck and Bolnick 2007). While more specialized individuals may experience improved foraging efficiency, they also become more susceptible to fluctuations in the limited set of resources they exploit (Bolnick et al. 2003; Dall et al. 2012). Consequently, the adaptive value of foraging specialization may vary over time and space due to fluctuations in factors such as competition levels or resource availability (van de Pol et al. 2010; Svanbäck et al. 2011; Sheppard et al. 2018). In fluctuating environments, different levels of individual niche specialization may persist within populations if, on average, they result in equal fitness (Svanbäck and Persson 2004). Quantifying individual niche variation and assessing its fitness consequences presents numerous challenges, as it necessitates measuring resource use and reproductive success over extended timeframes. Consequently, only a limited number of studies have attempted to do so to date (e.g., van de Pol et al. 2010; Cucherousset et al. 2011; Weimerskirch 2018). Numerous gull species have expanded their geographic range and ecological niche by capitalizing on new human-created food sources (Hunt and Hunt 1973; Spaans 1998; Ceia and Ramos 2015; Bond 2016). This expansion also applies to the European Herring Gull (Larus argentatus), a prevalent species along most of Europe's northwestern coastline. Over recent decades, Herring Gulls have successfully adapted to an increasingly industrialized environment, broadening their traditional diet of marine fish and invertebrates to include terrestrial food sources. These terrestrial sources primarily consist of vertebrates and invertebrates found in agricultural areas, made accessible by farming activities like mowing or ploughing, as well as human waste products prevalent in urban and industrial zones (Camphuysen 2013; Huig et al. 2016; Enners et al. 2018). Contrary to theoretical expectations, individual Herring Gulls generally exhibit a preference for a limited number of habitats, although there is significant variation in the degree of specialization among individuals (see also Ceia et al. 2014). Additionally, aside from habitat specialization, recent suggestions propose spatial segregation as a mechanism to reduce competition in a closely related gull species (Navarro et al. 2017). Site fidelity, as an added benefit, may enhance foraging efficiency by reducing the energy and time required for searching when food sources are reliable (Switzer 1993; Piper 2011; Patrick et al. 2014). Spatial specialization is particularly advantageous for Herring Gulls when feeding on human discards since the availability of such resources is often highly predictable in time and space, such as in rubbish bins or landfills.

The occurrence and adaptive value of spatial specialization may strongly depend on diet composition, thus linking it to the extent of habitat specialization by the individual. In this study, we evaluate the costs and benefits of foraging specialization in two Herring Gull colonies along the Belgian coast. By utilizing GPS tracking data from 31 breeding cycles involving 19 adult breeders (7 males and 12 females), we aim to establish a connection between foraging specialization and reproductive success. Initially, we quantify variations in habitat and spatial specialization (foraging site fidelity) among all GPS-tracked birds during incubation and chick rearing. Subsequently, we assess potential energetic and reproductive consequences of habitat and spatial specialization, using the average daily distance covered and offspring growth rates as proxies, respectively.

2. MATERIALS AND METHODS

DATA COLLECTION

Between 2013 and 2017, a total of 45 Herring Gulls were equipped with UvA-BiTS trackers (Bouten et al. 2013) during four breeding seasons in two colonies along the Belgian coast: Ostend (51.233°N, 2.931°E; 34 birds) and Zeebrugge (51.341°N, 3.182°E; 11 birds). The gulls were captured on their nests during incubation using clap nets or walk-in traps. Only one parent per nest was randomly selected for tagging, resulting in GPS data for single parents, except for one pair formed by two GPS-tracked birds that divorced from their original partners and paired up in the following year. The trackers were set to a 1–10-minute resolution during the breeding season, storing GPS positions and, starting from 2015, 10-second accelerometer readings. Nests were monitored twice a week to record laying dates, hatching dates, and chick weights (with 1-gram accuracy). The deployment of GPS trackers and the monitoring of eggs and nests were conducted in accordance with Flemish and Belgian legislation and were authorized by the ethical committees for animal experiments of Ghent and Antwerp University (ID numbers CDE 2013–73 and ECD 2012–51).

We retained data only from breeding birds with at least 5 days of at least 22 hours of GPS coverage per day during both incubation and chick rearing, and where at least 1 chick survived until 21 days of age, in a given year. The minimum of 5 days of data was enforced to ensure a proper estimation of habitat and space use consistency, while 22 hours of GPS coverage allowed for data retention even if some fixes were missing due to low battery power. This resulted in data from 7 males and 12 females, covering 31 breeding cycles. To avoid biases due to variation in tracking resolution, all GPS data were subsampled to a 10-minute resolution before behavioral assignment and analyses.

3. BEHAVIORAL INFERENCE

To quantify resource and spatial specialization, each GPS position was initially assigned to one of four behavioral classes: resting, present in the colony, commuting flight, or foraging. Assignments were based on habitat type information and accelerometer data associated with the GPS position or ground speed when accelerometer data were unavailable. Habitat type was derived from the 100 m-resolution CORINE land-cover database (European Environment Agency 2016). Ground speed cutoff values were determined based on the distribution of ground speeds for points with known behavior from accelerometer data.

Accelerometer readings were assigned to nine movement classes using a random forest classifier developed by Shamoun-Baranes et al. (2016). Ground speeds were used to discriminate between behaviors, with cutoff values set at 2 m/s to differentiate between flying and standing/walking, 0.17 m/s to distinguish between standing and walking, and 1.72 m/s to identify floating behavior at sea.

GPS fixes were classified as "present in colony," "resting," "commuting flight," or "foraging" based on the outlined criteria, considering both habitat type and movement characteristics. The distinction between foraging at sea and commuting flights above the sea was made based on track straightness, speed, and track patterns of fishing vessels. Fixes at sea, identified from CORINE land-cover data, were classified as "foraging" if specific criteria were met.

4. DATA ANALYSIS

ENERGETIC AND REPRODUCTIVE CONSEQUENCES

To evaluate the energetic and reproductive implications of habitat and spatial specialization, linear mixed effects models (LMM) were employed, with the year and bird identity as random effects. The average daily distance covered during incubation and chick-rearing served as a proxy for energy expenditure, representing foraging effort (Shamoun-

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Baranes et al. 2016). The LMM for distance covered incorporated fixed effects such as the average daily similarity in foraging habitat use, average daily change in foraging area, sex, and period, along with all possible 2-way interactions.

In exploring the interrelation between habitat and space use, additional LMMs were fitted with foraging area and average foraging distance during incubation and chick-rearing as response variables. Fixed effects included the average daily similarity in habitat use, average daily change in foraging area, sex, period, and their interactions.

To investigate the relationship between habitat or spatial specialization and offspring development, two LMMs were developed, using cumulative growth rates of the brood and individual chick growth rates as response variables. The models included fixed effects of average daily similarity in habitat use, average daily change in foraging area during the chick-rearing period, and the 2-factor interaction. The hatching rank of the chick and interactions with other predictor variables were added to the model for individual chick growth rates.

The random structure of the models was optimized using likelihood ratio tests, retaining bird identity as the sole random effect. Non-significant interaction terms were removed while retaining main effects. The significance level was set at 95%, and model residuals were visually assessed for normality, homoscedasticity, and independence All analyses were performed in R version 3.4.2 (R Core Team 2017), and LMMs were fitted using the nlme package (Pinheiro et al. 2018). Marginal means for factorial variables were calculated using the lsmeans package (Lenth 2016).

5. RESULTS

In our study population, Herring Gulls displayed substantial variation in habitat specialization, ranging from highly specialized to more generalist individuals in both sexes While urban/industrial and coastal habitat specialization were notable, none of the tracked birds exhibited specialization in agricultural habitats. Spatial specialization showed less variation, with most individuals covering large foraging areas and changing sites over consecutive days.

Movement patterns were significantly related to habitat and spatial specialization. Individuals with higher levels of habitat specialization covered shorter daily distances on average, exploiting smaller foraging areas located closer to the breeding colonies. The average daily distance covered was not associated with individual spatial specialization, and the size of the foraging area did not correlate with average daily changes in foraging locations. However, individuals with higher spatial specialization foraged closer to the colony, using smaller foraging areas and covering shorter distances during incubation. The effects of habitat and spatial specialization on foraging movements did not differ between sexes.

6. CONCLUSION

In this investigation, we undertook a comprehensive assessment of individual spatial and habitat specialization in 19 GPS-tagged Herring Gulls, aiming to elucidate whether foraging specialization during the breeding season contributes to improved foraging efficiency and subsequent offspring development. Our findings highlight a positive association between higher levels of habitat specialization and reduced average daily distances covered, leading to accelerated nestling growth. Consequently, our study provides empirical evidence for the fitness implications of foraging specialization within a generalist bird species.

Foraging specialization is recognized for its potential to mitigate intraspecific resource competition (e.g., Bolnick 2001; Svanbäck and Bolnick 2007), making it particularly relevant in colonial breeders where large numbers of individuals congregate during reproduction, as observed in seabirds (Ceia and Ramos 2015). Specialization in foraging may manifest as preferences for specific resources, habitats, or locations, which are not necessarily correlated or mutually exclusive (Navarro et al. 2017). Prior studies on Herring Gulls predominantly emphasized positive effects of specialization related to nutritional quality, particularly in foraging on high-calorific food sources like fish (Bukacińska et al. 1996; van Donk et al. 2017). Benefits of spatial specialization have also been documented in various seabird species, contributing to the reduction of time and energy spent searching for prey and alleviating competition at foraging sites (Patrick et al. 2014; Navarro et al. 2017). Our simultaneous assessment of habitat and spatial specialization in this study reveals their interconnected nature in the Herring Gull population. Higher consistency in foraging habitat use correlates with smaller foraging areas and shorter travel distances, highlighting the intertwined relationship between the two dimensions .Despite displaying consistent variation in habitat use, spatial specialization was generally low in our study population and did not correlate with energetic costs of foraging, consistent with recent findings in a Dutch population (van Donk et al. 2018).

Observations indicate that Herring Gulls adjusted their foraging movements, but not their diet, between incubation and chick rearing. Both sexes tended to cover shorter distances on average and forage within smaller areas closer to breeding colonies during incubation. While increased distances covered during chick rearing could be directly attributed to the demand for feeding chicks, leading parents to undertake multiple foraging trips per day, this doesn't explain the change in foraging area. The biparental care provided by Herring Gulls, coupled with high territory attendance during incubation, may impose time constraints, limiting foraging to proximity of the colony to avoid potential egg predation (Niebuhr 1983). Alternatively, resource availability might be more abundant close to the breeding colony early in the breeding season, gradually diminishing during chick rearing. Shifts in habitat use between incubation and chick rearing within individuals were limited, reinforcing the complex dynamics of foraging strategies during different phases of the breeding season.

Our findings shed light on the impact of foraging specialization on chick growth in a long-lived seabird. The renewed interest in understanding how such variability influences population dynamics has been gaining traction among behavioral ecologists. Individual variation is increasingly acknowledged as a pivotal driver of eco-evolutionary processes (Bolnick et al. 2011; Kokko et al. 2017). While previous studies on individual specialization predominantly focused on short-lived species, revealing selection for niche divergence in response to intraspecific competition (e.g., Bolnick 2001; Araújo et al. 2008), recent advancements in high-resolution GPS tracking now enable the examination of foraging strategies in long-lived species throughout their entire lifespan (Hussey et al. 2015; Kays et al. 2015).

The incorporation of tracking technology allows researchers to move beyond dietary differences (van Donk et al. 2017) and explore the consequences of spatial specialization, linking assessments of foraging effort to reproductive success. Although our results demonstrate positive fitness outcomes of specialized foraging strategies over our 5-year study duration, Herring Gulls boast a potential lifespan of up to 20 years (Camphuysen 2013). Environmental changes may introduce variations in the costs and benefits of different strategies over such extended timeframes (Bennett et al. 2017). Therefore, long-term studies become essential to determine whether the energetic and fitness advantages of foraging strategies fluctuate over time. This is crucial for understanding the cost-benefit trade-offs that sustain the coexistence of specialist and generalist strategies within a population (Svanbäck and Persson 2004).

GPS tracking not only opens up exciting prospects for investigating foraging strategies in long-lived species but also provides a unique lens to explore how individual variation in strategies may shape long-term population dynamics. Additionally, it allows researchers to assess whether these dynamics are influenced by the anticipated rapid environmental changes.

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