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Inter-colony variation in the foraging behaviour and resource selection of breeding Herring Gulls *Larus argentatus*

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Abstract

The resources available to breeding seabirds within their foraging ranges can influence productivity, either directly through the quality and quantity of food consumed by chicks, or indirectly by affecting the foraging behaviour and efficiency of parent birds. Where local resource availability is low, or the quality of resources is poor, species with flexible time–energy budgets can increase their foraging effort to provide adequate energy and nutrients to their chicks, although this may come at the expense of nest attendance. We investigated provisioning rates and nest attendance in European Herring Gulls *Larus argentatus* from seven colonies across southwest Scotland and Northern Ireland during two chick-rearing periods (2013 and 2014) in relation to the food resources used by these colonies. We observed variation in provisioning rates and nest attendance between colonies, and variation between years in nest attendance. We found no significant relationships between these behaviours and the proportion of intertidal prey consumed, suggesting that provisioning rate and nest attendance did not differ between resource types at the colony level. We also found no evidence that variation in behaviours was related to breeding success. Our results suggest that, within this region, the type of resources consumed had a greater influence on Herring Gull breeding success than differences in two proxies of foraging efficiency (provisioning rate and nest attendance), although other factors may also have influenced breeding success. Our work highlights the benefit of determining what food resources are provided to chicks, in addition to measuring foraging behaviours, to fully understand the consequences of consuming different resources on the breeding success of generalist foragers.

Introduction

To understand drivers of population change it is important to establish how species use the resources in their environment (Johnson 1980). Food is a particularly important resource and individuals will select food sources within their foraging range based on its availability and profitability, ensuring the maximum benefit for the lowest cost (Pulliam 1974). Changes in food resources can therefore affect population dynamics (reviewed in White 2008). For example, local food resources can be particularly limiting for breeding seabirds that are generally colonial and constrained to a central nesting site (White 2008), resulting in intra- and inter-specific competition for local food resources, which can influence a population's demography (Ashmole 1963; Furness & Birkhead 1984; Birt *et al.* 1987). Learning how seabirds use local food resources under different conditions can help us better understand how food resources influence population size.

Behaviours associated with a species' foraging strategy can show great plasticity, influenced by the availability, quality and distribution of food resources (Pyke 1984). As well as variation in availability, and energetic and nutritional quality, different resources may also differ in the time and energy it takes to obtain them, which may influence parental foraging behaviours (Tremblay *et al.* 2005; Burke & Montevecchi 2009; van Donk *et al.* 2019). The ability to flexibly adjust their foraging in response to changes in resources can allow individuals to buffer their breeding output, making foraging behaviour a good candidate through which to identify environmental changes (Cairns 1987). As the distribution and availability of resources can change with a changing environment, parents may have to switch to alternative food sources to provision their young. This is especially true of generalists, which can forage on multiple resources within their foraging ranges. Alternative food sources may be less profitable in energy or nutrients, or more costly for parents to gather due to longer search, capture and/or handling times (Burger & Piatt 1990; van Donk *et al.* 2019). This may necessitate longer foraging trips and result in reduced provisioning rates (Hamer *et al.* 1993; Quintana 2008; Rishworth & Pistorius 2015). Increasing foraging time can also reduce nest changeovers, with fewer instances of both parents attending the nest simultaneously, and increase the overall nest attendance of at least one parent. Reduced nest attendance can result in higher predation risk and the exposure of chicks to unfavourable weather, and hence lower productivity (Uttley *et al.* 1992; Hamer *et al.* 1993; Wanless *et al.* 2005; Ashbrook *et al.* 2008; Chivers *et al.* 2012). Differences in the main food resource exploited can therefore affect how long adults spend away from the nest, and hence variation in nest attendance and provisioning rates (Bijleveld & Mullers 2009). In seabirds, adult behaviours related to offspring care, including provisioning rates and nest attendance, can be readily observed at the nest (Uttley *et al.* 1992; Wanless & Harris 1992; Kitaysky *et al.* 2000; Chivers *et al.* 2012). Therefore, as foraging behaviours can influence chick survival and productivity, they can be useful in revealing the pressures acting on the resources and habitats that seabirds rely on (Berger-Tal *et al.* 2011).

The *Laridae* gulls form a group of generalist seabirds of which several species typically consume a wide variety of resources from both marine and terrestrial environments (Hunt & Hunt 1973; Kubetzki & Garthe 2003). Large gulls generally forage on the most available resources within their foraging range and the type of resources provisioned to chicks can subsequently influence their breeding success (Pons 1992; Annett & Pierotti 1999; van Donk *et al.* 2017). For example, in southwest Scotland and Northern Ireland, colonies of European Herring Gulls *Larus argentatus* (hereafter 'Herring Gull') that consumed higher proportions of intertidal prey had larger brood sizes than colonies where individuals consumed more terrestrial resources (predominantly grain as well as invertebrates and anthropogenic food items; O'Hanlon *et al*. 2017). Discrepancies in breeding success were attributed to intertidal resources being of higher quality than the available terrestrial resources (O'Hanlon *et al*. 2017). Although the energy density and lipid content of intertidal prey may not be as high as that of fish and some domestic refuse, it can contain specific nutrients that are important for chick growth such as calcium (Annett & Pierotti 1989; Noordhuis & Spaans 1992; van Donk *et al*. 2017). Alternatively, intertidal prey may have been more abundant or accessible to the gulls from colonies that consumed a higher proportion of this resource, resulting in higher provisioning rates or nest attendance (Lamb *et al*. 2017).

Here we investigate variation in nest attendance and provisioning rates among Herring Gull colonies across southwest Scotland and Northern Ireland over two breeding seasons in relation to the food resources used by these colonies (based on the results of pellet analysis reported in O'Hanlon *et al*. 2017). Specifically, we hypothesise that if intertidal resources are more abundant or accessible, allowing gulls to forage more profitably, adults in these colonies will have increased provisioning rates and/or higher nest attendance. If, however, it is the *quality* of intertidal resources that affects breeding success, the relationship between the proportion of intertidal prey in the diet and a colony's breeding success would not be affected by provisioning rates and/or nest attendance. These results will add to our understanding of what factors influence gull breeding success across a range of colonies.

Methods

Study area

We studied seven Herring Gull colonies during the 2013 and 2014 breeding seasons (Table 1, Figure 1). Colonies were situated along a gradient of human population density and were surrounded by different foraging habitats (O'Hanlon *et al*. 2019). We carried out nest observations at each colony in both breeding seasons to record parental care behaviours (nest attendance and provisioning rate) and breeding success. We obtained colony-level data on the resources consumed by analysing fresh pellets collected from known Herring Gull territories during the pre- and post-hatching periods (as described in O'Hanlon *et al*. 2017).

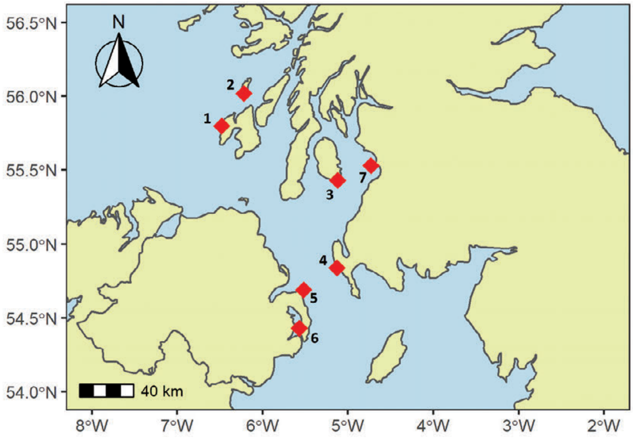

Figure 1. Location of the seven Herring Gull *Larus argentatus* breeding colonies across southwest Scotland and Northern Ireland included in this study. 1: Islay; 2: Oronsay; 3: Pladda; 4: Portpatrick; 5: Copeland Islands; 6: Strangford Lough (Green and Round Islands); 7: Lady Isle. Colonies are numbered according to a gradient of lowest (Islay) to highest (Lady Isle) amount of built-up area within 50 km of the colony as a proxy of human population density (O'Hanlon *et al*. 2019).

Table 1. The mean provisioning rate and nest attendance of Herring Gull *Larus argentatus* per year during chick rearing for the seven colonies across southwest Scotland and Northern Ireland. Also shown are the number of observational hours and total number of nests observed, mean brood size and the proportion of pellets containing intertidal items. Colony size refers to the number of apparently occupied nests (AON), year of count given in parenthesis. The number of nests used to estimate mean brood size is given in parenthesis, as is the total number of pellets collected.

Colony	Year	Colony Size	Mean brood size	Proportion of pellets containing intertidal items	Nests observed	Observation hours	Mean provisioning rate per three-hour watch	Mean proportion of time nests were left unattended per hour
Copeland[1]	2013	683 (2012)	1.67 (6)	0.00 (21)	11	171	0.90	0.00
	2014		2.33 (12)	0.06 (106)	36	447	0.78	0.09
Islay	2013	25 (2013)	1.43 (7)	0.16 (87)	17	387	0.78	0.07
	2014		1.75 (4)	0.13 (40)	8	263	0.44	0.38
Lady Isle	2014	831 (2012)	na	0.06 (70)	19	117	1.03	0.10
Oronsay	2013	95 (2013)	1.73 (15)	0.52 (62)	18	486	1.06	0.09
	2014		2.00 (9)	0.40 (30)	34	312	0.49	0.17
Pladda	2013	150 (2013)	1.77 (22)	0.08 (102)	40	588	1.03	0.17
	2014		na	0.14 (111)	33	255	0.86	0.11
Portpatrick	2013	175 (2013)	1.64 (11)	na	15	345	1.51	0.04
	2014		1.87 (30)	0.02 (49)	66	849	1.30	0.06
Strangford[2]	2013	190 (2013)	2.09 (11)	0.40 (5)	25	240	0.58	0.00
	2014		2.20 (15)	0.40 (50)	41	381	0.85	0.12

[1] Observational watches completed on Lighthouse Island however, colony size is for the three Copeland Islands combined due to their proximity (<1.5 km).

[2] Watches at Strangford were undertaken at two sites within 7 km of each other (Round Island and Green Island in 2013, Green Island in 2014). Colony size is an average from Green Island (115 AON) and Round Island (265 AON).

Nest observations

Herring Gull colonies were visited on multiple occasions throughout the chick-rearing period between 1 June 2013 to 16 July 2013 and 3 June 2014 to 4 July 2014. We visited each colony on an average of six dates across each breeding season (range 2–14) and conducted multiple watches on each visit. We define a watch as a three-hour observation period from a specific vantage point, using an observation hide where necessary. This allowed us to observe up to 24 focus nests simultaneously whilst not causing disturbance to the birds. We included only nests that had an unobstructed view from the vantage point and were identified as Herring Gull nests from observing the attending adults. Where possible, we carried out watches from the same vantage point hence making multiple observations of the same nests. Watches were scheduled across daylight hours between 06.00 and 20.00, categorised into morning (06.00–10.00), midday (10.00–14.00) and afternoon/evening (14.00–20.00). Each watch was also categorised as high tide (within three hours of peak tide), low tide (within three hours of peak low tide) or slack tide (watches outside of three hours of peak low or high tide). We ensured that watches were carried out across the different stages of tide as this can influence availability of intertidal prey. We carried out all watches in no rain or light rain and with the sea state/wind below a Beaufort scale of five. Timing of hatching was similar across colonies and years (O'Hanlon & Nager, pers. obs), and the dates of watches did not differ between colonies (ANOVA: $F_{6,73} = 1.034$, $P = 0.411$) or years ($F_{1,73} = 0.006$, $P = 0.940$). Chicks were therefore observed at comparable stages across colonies and years.

During each watch we recorded the number of Herring Gull chicks present at each nest (brood size) and scanned nests every five minutes to record whether zero, one or two adults were attending the territory. We recorded gulls as attending a territory if they were present on the nest, in close proximity to the nest and positively interacted with the chicks or other attending adult (if present), or present in close proximity to a nest in an area known to be part of the territory from previous observations. We defined nest non-attendance as the proportion of time per nest per watch where no adult was present on the territory. Provisioning of chicks was recorded when it occurred. When chicks were provisioned on more than one occasion within the same watch a new provisioning event was only recorded if that adult had left the territory and completed another foraging trip (minimum time away: 20 minutes), or if the chicks were fed by the other returning adult. Herring Gull observation watches were carried out by eight observers: four in 2013 and five in 2014, including one observer across both years, with no detectable difference between observers after accounting for number of chicks, year and date (O'Hanlon 2016).

Resource Use

Herring Gull pellets were collected from each colony during the pre- and post-hatching period of 2013 (N = 277) and 2014 (N = 456). Food remains contained in the pellets were identified as terrestrial (grain, invertebrates, bird and mammal remains plus anthropogenic items such as plastics and glass indicative of feeding in terrestrial habitats), intertidal (marine crustaceans, molluscs and echinoderms) or offshore marine (fish species and *Nephrops sp.*; Appendix 1, O'Hanlon *et al*. 2017). We scored each food item based on whether it made up 25% or more of a pellet's bulk or not. We then calculated the frequency of occurrence of each resource category (terrestrial, intertidal and offshore marine) as the number of pellet samples scored as over 25% of the pellet's bulk for that resource category, divided by the total number of pellet samples (Duffy *et al*. 1986). We pooled the pellets for each colony and year, as we found no difference in pellet contents between years or pre- and post-hatching periods (O'Hanlon *et al*. 2017). Most diet items found in the pellets were categorised as from either intertidal or terrestrial sources and the gulls' use of resource categories based on our pellet analysis matched well with the resource categories assimilated into growing feathers as measured with stable isotopes (O'Hanlon *et al*. 2017). At the colony-year level, the proportion of pellets containing intertidal and terrestrial items was correlated (Pearson's correlation: $r = -0.75$, $P = 0.005$, $N = 12$), and so we used the proportion of intertidal items to relate provisioning rates and nest attendance to resource use.

Productivity

To determine whether inter-colony differences in provisioning rates and nest attendance were associated with the Herring Gulls' breeding success, we related the means of these two parental care behaviours to the final brood size of nests that could still be observed three or more weeks after hatching (O'Hanlon *et al*. 2017). We used final brood size as a measure of breeding success as chicks of at least three weeks old are likely to successfully fledge (Bolton 1991).

Analysis

We performed all statistical analyses in R, Version 4.0.3 (R Core Team 2020). At the colony-level, we investigated the relationships between mean annual provisioning rates and nest attendance using a Pearson's product-moment correlation to establish whether the two behaviours were related ($N = 13$). We also repeated this at the nest-level by performing a general linear mixed effect model (GLMM) with a Conway-Maxwell-Poisson error distribution, using the *glmmTMB* package (Brooks *et al*. 2017). 'Provisioning rate' was the response variable, while 'attendance', 'year' and their interaction were fixed effects, and 'nest ID' and 'watch' were random effects.

To determine whether time of day or tidal state affected the Herring Gulls' foraging behaviour we ran two GLMMs. 'Time of day' and 'tidal state' were included as fixed effects, 'colony' and 'year' as random effects, and 'nest attendance' or 'provisioning rate' as the response variables. To model 'nest attendance' we used the proportion of time no adults were present at the nest (subsequently referred to as 'nest non-attendance') as the response variable, which included 51% zero values for nest non-attendance. We logit transformed nest non-attendance values so that the residuals met the normality assumption after first adding 0.01 to all values due to the presence of zero values.

To investigate inter-colony and interannual variation in provisioning rates and nest attendance, we carried out separate GLMMs with each of the two behaviours as the response variables. Provisioning rate was fitted with a Conway-Maxwell-Poisson error distribution and log link function to account for under dispersion (Lynch *et al*. 2014). Logit transformed nest non-attendance was fitted with a Gaussian error distribution. In both models, 'colony' and 'year' were fixed effects, and 'nest ID' and 'watch' were random effects. An interaction between colony and year could not be included as the resulting model was rank-deficient and so we ran separate GLMMs for each year to explore inter-colony differences. To explore which colonies differed from each other we carried out Tukey post-hoc tests using the 'glht' function in the *multcomp* R package (Hothorn *et al*. 2008).

To establish whether provisioning rates and nest attendance were related to the proportion of intertidal items in the diet, separate linear models were conducted with the proportion of pellets that contained intertidal items (as proxy for intertidal resource use) and colony size included as explanatory variables. Colony size was included to account for potential competition for food resources resulting in local resource depletion in proximity to larger colonies (Furness & Birkhead 1984; Birt *et al*. 1987). The values of the parameters used to evaluate the behaviours were averaged per colony and year, and therefore data were available for 12 colony-years (no pellet data were available for Portpatrick or Lady Isle in 2013 with no foraging behaviour observations on Lady Isle in 2013).

To determine whether breeding success (number of chicks that were at least three weeks old and therefore were assumed to have fledged) at the nest level was related to provisioning rate and nest attendance, we used a GLMM with 'brood size' as the response variable, 'provisioning rate' and 'nest attendance' as fixed effects and 'colony' and 'year' as random effects. We only used nests that had been observed over at least three watches until the chicks were near fledgling size, and behaviours were averaged across watches; data were therefore available for 142 nests (72 nests from six colonies in 2013 and 70 nests from five colonies in 2014, as no nests were observed on three or more watches on Pladda and Lady Isle). For this analysis, we used nest attendance where at least one adult was present at the nest. We related whether a nest had lost a chick or not to the mean provisioning rate at that nest using a GLMM with binomial error structure and 'colony' as a random effect. As some nests may have lost a chick before our first watch, we only included nests where three chicks were present during the first watch (N = 62 across all colonies and years). For nests which lost chicks between subsequent watches, we used only the provisioning rates from watches when all three chicks were still present.

We checked diagnostic plots to ensure all model assumptions were met. Significance thresholds were set at two-tailed $P < 0.05$. We calculated $R^2_{GLMM(m)}$ (the 'marginal' R^2 value, the proportion of the variance in the response variable that is explained by the explanatory variables; Johnson 2014) using the R package *MuMIn* (Barton 2012). Mean ± standard deviation values are reported.

Results

We calculated mean nest non-attendance and provisioning rates for 28 ± 16 nests and 12 ± 4 observation watches per colony (Table 1). There was no correlation between mean provisioning rates and nest attendance at the colony level ($r = 0.48$, $P = 0.097$, $N = 13$). However, there was a significant positive relationship between provisioning rate and nest attendance at the nest level ($\chi^2_1 = 13.06$, $P < 0.001$; $R^2_{GLMM(m)} = 0.01$; with no statistically significant effect of year, $P = 0.17$), with higher provisioning rates associated with higher nest attendance.

Neither provisioning rate nor nest attendance was related to the time of day (provisioning rate: $\chi^2_2 = 0.03$, $P = 0.99$; nest non-attendance: $\chi^2_2 = 2.73$, $P = 0.26$) or tidal state (provisioning rate: $\chi^2_2 = 3.40$, $P = 0.18$; nest non-attendance: $\chi^2_2 = 02.22$, $P = 0.33$). Therefore, we did not include these variables in further analysis of the gulls' provisioning rate or nest attendance.

We found that nest non-attendance differed between colonies and years (colony: $\chi^2_6 = 93.05$, $P < 0.001$; year: $\chi^2_1 = 11.80$, $P < 0.001$; $R^2_{GLMM(m)} = 0.13$). Nests were left unattended for a lower proportion of time in 2013 (0.08 ± 0.17) than in 2014 (0.13 ± 0.20). Variation in nest non-attendance between colonies occurred in 2013 ($\chi^2_5 = 95.07$, $P < 0.001$; $R^2_{GLMM(m)} = 0.19$) and 2014 ($\chi^2_6 = 41.82$, $P < 0.001$; $R^2_{GLMM(m)} = 0.14$). The inter-colony variation in nest non-attendance in 2013 was largely driven by Pladda having nests left unattended for a greater proportion of time than in all other colonies (Figure 2a), whilst in 2014 Islay had nests left unattended for a greater proportion of time compared to all other colonies (Figure 2b).

Provisioning rate varied between colonies ($\chi^2_6 = 63.91$, $P < 0.001$, $R^2_{GLMM(m)} = 0.10$), largely driven by Portpatrick which had higher provisioning rates than all other colonies except Lady Isle (Figure 3). Provisioning rate in 2013 (1.01 ± 0.92 provisioning events per three hours) appeared to be higher than in 2014 (0.91 ± 0.95 provisioning events per three hours) but the difference was not statistically significant ($\chi^2_1 = 71.00$, $P = 0.097$).

The inter-colony variation in provisioning rates and nest attendance was not related to the proportion of intertidal items in pellets (provisioning rate: $F_{1,11} = 2.39$, $P = 0.152$; nest attendance by at least one adult: $F_{1,11} = 0.03$, $P = 0.878$). Colony size was not significant in either model ($P = 0.241$).

Productivity, measured as number of chicks more than three weeks old, was significantly related to provisioning rate ($\chi^2_1 = 5.255$, $P = 0.022$, $R^2 = 0.04$) but not nest attendance by at least one adult ($\chi^2_1 = 0.432$, $P = 0.511$). Nests which had three chicks of at least three weeks of age had a higher provisioning rate (1.19 ± 0.74 provisions h^{-1}, $N = 27$) than nests that had two (0.96 ± 0.62 provisions h^{-1}, $N = 72$) or one chick (0.88 ± 0.59 provisions h^{-1}, $N = 43$). This was likely due to larger broods requiring more frequent provisioning as among the nests that had three chicks during the first watch there was no significant difference in provisioning rates between nests that lost a chick in subsequent watches to those that raised all three chicks ($\chi^2_1 = 1.21$, $P = 0.27$).

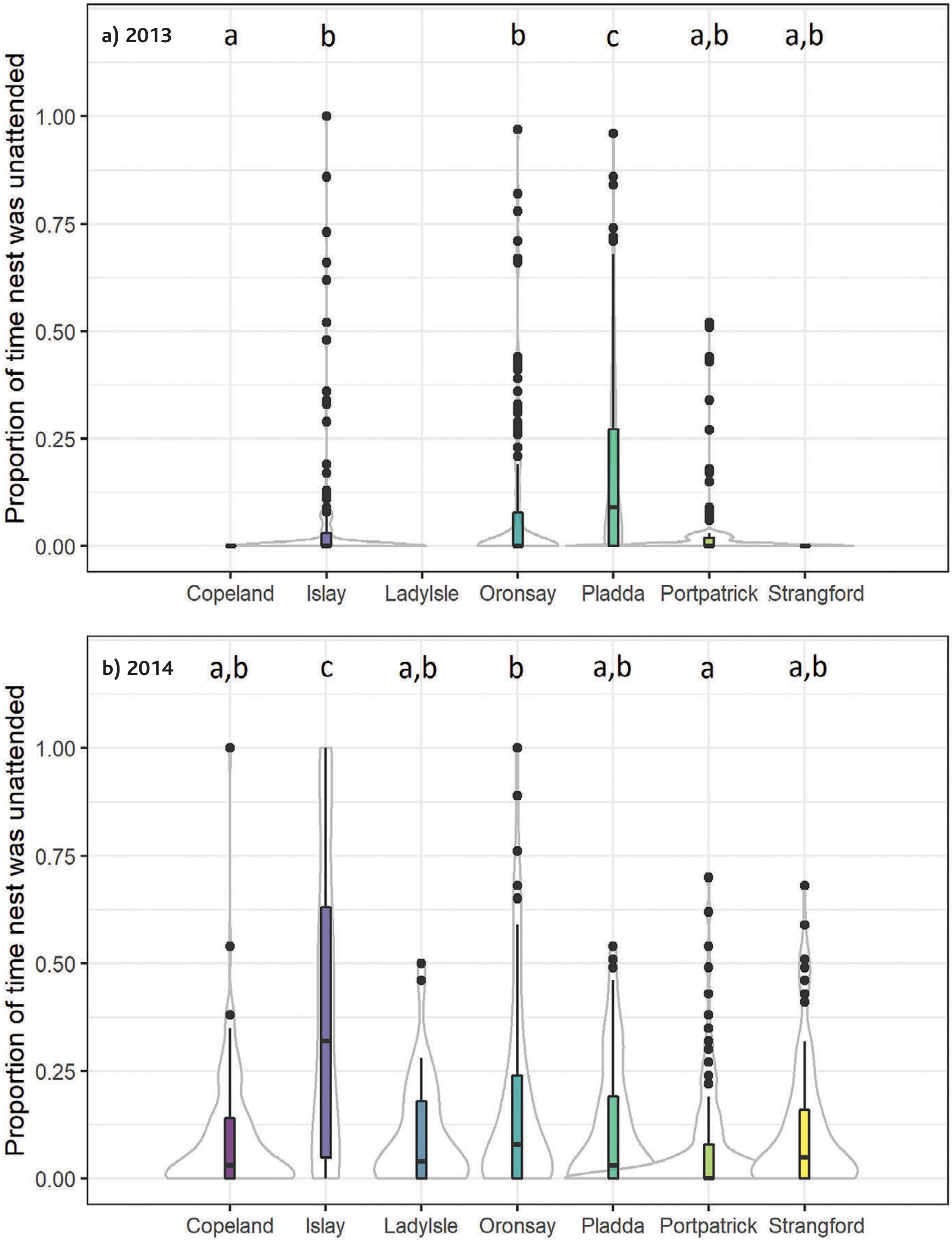

Figure 2. Proportion of nest non-attendance per hour by Herring Gulls *Larus argentatus* at seven colonies in southwestern Scotland and Northern Ireland in **a)** 2013 and **b)** 2014. Boxplots show median (horizontal line), inter-quartile ranges (box), minimum and maximum values (whiskers) and outliers (black dots); violin plots (grey line) outline the full distribution of the data. Colonies with different letters above the boxes are significantly different from each other in that year (Tukey's HSD post-hoc multiple comparisons P < 0.05).

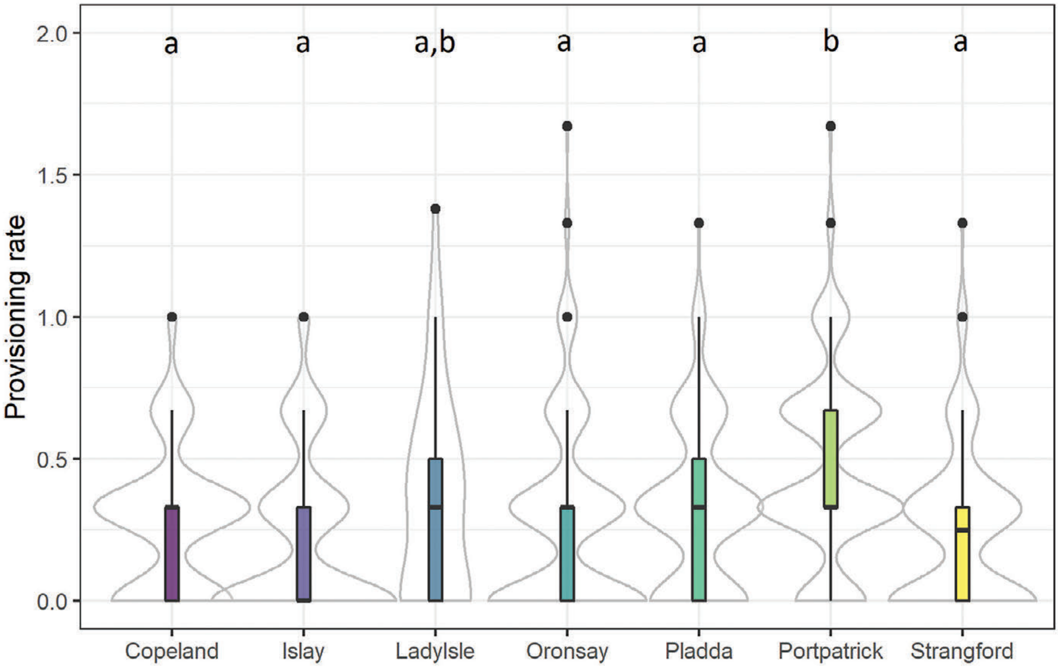

Figure 3. Provisioning rates of Herring Gulls *Larus argentatus* across seven colonies in southwest Scotland and Northern Ireland (number of provisioning events per three-hour watch during the 2013 and 2014 breeding seasons). Boxplots show median (horizontal line), inter-quartile ranges (box), minimum and maximum values (whiskers) and outliers (black dots). Violin plots (grey line) show the full distribution of the data. Colonies with different letters above the boxes are significantly different from each other (Tukey's HSD post-hoc multiple comparisons P < 0.05).

Discussion

Across the seven Herring Gull colonies in southwest Scotland and Northern Ireland, we found variation in nest attendance and provisioning rates. There was also variation in nest attendance between years, but the difference in provisioning rate between years was not statistically significant. Thus, it is possible that the Herring Gulls maintained provisioning rates between years at the expense of nest attendance. We found no evidence that provisioning rates and nest attendance were related to the proportion of intertidal resources a colony consumed or to the gulls' breeding success. Herring Gulls experienced higher breeding success at colonies where they consumed more intertidal resources (O'Hanlon *et al.* 2017) and our results indicate that this was likely the result of the quality (energy and nutrient content) of the intertidal prey rather than the gulls' foraging efficiency when acquiring this resource.

We found that provisioning rates and nest attendance varied across the seven study colonies likely because of the different types of resources that were consumed at each colony (Appendix 1). Observations at the colonies were carried out across different times of day and tidal states to account for variation in the gulls' behaviour with respect to these factors (Sibly & McCleery 1983; Enners *et al.* 2018). Timing of observations did not differ between colonies or years, nor was there evidence to suggest that gulls preferentially provisioned chicks at certain times of day or tidal states. Gulls' foraging is often related to time of day and tidal state; however, this will depend on the resources the gulls are exploiting (Sibly & McCleery 1983; Yoon *et al*. 2014; Enners *et al*. 2018). Across the study colonies, Herring Gulls differed in the range of resources they foraged on and consumed multiple resource types that are available at different tidal states and times of day (O'Hanlon *et al*. 2017; Appendix 1). This may explain why we detected no relationships with tidal state or time of day across colonies. The classification of food sources as 'terrestrial', 'intertidal' or 'offshore marine' may have been too coarse to identify more subtle differences in foraging rates between different food sources. Additionally, our three-hour watches may have been too short to pick up temporal pattens in foraging in relation to time of day or tide. Colony size is also known to affect gull foraging behaviour, as local prey depletion and increased competition from conspecifics in larger colonies can increase foraging trip durations, as individuals need to forage further from the colony (Lewis *et al*. 2001; Davoren & Montevecchi 2003; Ballance *et al*. 2009). At the colony level we found no evidence for any influence of colony size on provisioning rate or nest attendance, but the number of nests observed was relatively small and hence the statistical power was low.

The inter-colony variation in nest attendance and provisioning rates was largely driven by a small number of colonies. Provisioning rates were largely similar across colonies except for Portpatrick which had higher provisioning rates than other colonies with Herring Gulls almost exclusively consuming terrestrial items, particularly grain obtained from farmland, which is a low-quality food resource for breeding gulls (O'Hanlon *et al*. 2017). This suggests that breeding gulls in Portpatrick may have compensated for the low quality of their food by increasing their provisioning rates to meet the energy and nutrient requirements of chicks. Indeed, as the Portpatrick colony was located close to farmland where the gulls could forage for grain, short trips between foraging sites and the nest may have also contributed to the observed high provisioning rate at that colony. Increasing offspring provisioning effort may come at the expense of reduced nest attendance therefore nest attendance may be lower when parents increase their foraging effort to maintain adequate provisioning rates (Cairns 1987; Burger & Piatt 1990; Smout *et al*. 2013). However, this is unlikely to be the case here as at the nest-level higher provisioning rates corresponded with high nest attendance by at least one adult, and there was no correlation between provisioning rates and nest attendance at the colony level.

Arguably, the highest quality food resources for Herring Gulls are fishery discards and refuse from landfill sites (van Donk *et al*. 2017). However, most colonies within the study region had no access to large amounts of fishery discards, large landfill sites, or built-up areas where they could scavenge for food. The exceptions were Pladda, where gulls had access to discards from local *Nephrops* sp. fishing activities, and Lady Isle, which is located near to built-up areas, resulting in access to abundant refuse (O'Hanlon *et al*. 2017). Lady Isle and Pladda had the highest provisioning rates after Portpatrick, with the provisioning rate at Lady Isle being comparable to that at Portpatrick. This suggests that fishery discards and refuse resources may be collected efficiently allowing for a high provisioning rate. However, Pladda also had low nest attendance in 2013 (although not 2014), suggesting that despite the high quality of fishery discards, there may be disadvantages to foraging on this resource, including greater competition, search times and handling times (van Donk *et al*. 2019). This suggests that in a generalist forager, the distribution or availability of alternative food sources may be as important in influencing variation in provisioning rate as the attributes of the most profitable food source.

Nest attendance, and to a lesser extent provisioning rates, differed between the 2013 and 2014 breeding seasons, with both being lower in 2014. This was particularly noticeable for Herring Gulls in Islay where nests were unattended for a much greater proportion of time in 2014. This may be indicative of foraging conditions being more challenging across the region in 2014, resulting in the gulls increasing their foraging effort to the extent that nests were left unattended for a greater proportion of time. That provisioning rates did not differ significantly between the two years suggests that Herring Gulls were flexible in their time-energy budgets and able to increase their time spent foraging, despite variation in resource availability, as had been reported in other seabird species (e.g. Burger & Piatt 1990; Harding *et al*. 2013; Smout *et al*. 2013). Despite lower nest attendance and provisioning rates in 2014, mean brood size was higher in 2014 than in 2013 (O'Hanlon *et al*. 2017). This discrepancy between indices of foraging effort and breeding success suggests that instead of foraging behaviour influencing productivity, resource use might have been a larger driver. Gulls in colonies provisioning chicks with more intertidal resources did not differ in provisioning rate or nest attendance from gulls in colonies predominantly exploiting alternative resources. If intertidal prey was not generally the most profitable in terms of energy, gulls foraging on this resource would need to provision their chicks more frequently to ensure the chicks received adequate energy to successfully fledge. This was not found however, suggesting that intertidal prey is a high-quality food source for breeding gulls.

The relationship that we found between higher provisioning rates and larger final brood sizes was likely due to the higher energy demand of larger broods (Weimerskirch *et al*. 1995; Ratcliffe & Furness 1999). If a higher provisioning rate resulted in greater breeding success, we would expect a lower provisioning rate to relate to chick loss. However, this was not observed and no difference in provisioning rates were observed within a sub-sample of three-brood nests that subsequently lost chicks in comparison to a sub-sample where all chicks survived to fledgling age. We found no evidence that resource type was correlated with provisioning rates or nest attendance. Instead, the type of food items provided to chicks appeared to be more important in influencing breeding success than provisioning rates and nest attendance. Our results therefore indicate that differences in behaviour associated with foraging on different resources did not directly influence the gulls' breeding success, and productivity may instead be attributed to intertidal food resources containing important nutrients, such as calcium (O'Hanlon *et al*. 2017). In contrast, Hunt (1972) found that higher chick loss was associated with increased parental American Herring Gull *L. smithsonianus* foraging behaviour across colonies in a region of the east coast of America (Hunt 1972). However, it should be noted that many factors can affect breeding success such as weather, predation, and disturbance in colonial birds (Burger 1982), and we did not account for these. Furthermore, the number of study nests per colony and year within this study were relatively low, and therefore may not have been representative of what was occurring at the colony-level. Future studies should seek to consider what resources individual Herring Gulls consume and relate this to foraging behaviour, including trip duration, through methods such as GPS tracking and dietary analysis via pellets or stable isotopes (e.g. Bukaci´nski *et al*. 1998; Ceia *et al*. 2014; Brisson-Curadeau *et al*. 2017). Our three-hour watches were not long enough to capture reliable estimates of trip durations. Furthermore, variation in provisioning rates may also be buffered by gulls increasing the size of their meals rather than increasing the number of provisioning events (Oro *et al*. 1997; Burke & Montevecchi 2009), however, we were unable to quantify the size of provisions to chicks from our nest observations. Understanding the resource use of a species can help determine factors influencing their demography (Davoren & Montevecchi 2003) as well as identifying particular prey species or foraging areas that need protection (Hooker & Gerber 2004; Louzao *et al*. 2008). Herring Gulls are opportunistic generalist foragers, that will exploit a variety of available habitats and different food sources within their foraging ranges. Specific resource types can differ in their search, capture and handling times (i.e. foraging efficiencies), abundances and energetic and nutritive qualities across space and time. These differences likely contribute to the large variation in the preferred foraging habitats and food sources that we observed among colonies and regions in Herring Gulls, as well as how these affect their demography. Within our study region, intertidal resources are important for breeding Herring Gulls, likely due to their quality rather than them being more easily accessible. Thus, the population-level influences of habitat composition and resource around gull colonies requires further attention (Matthiopoulos *et al*. 2019). Our results highlight the value of identifying the types of resources that species consume as well as the foraging behaviours associated with different food resources, when inferring the importance of different habitats for generalist species.

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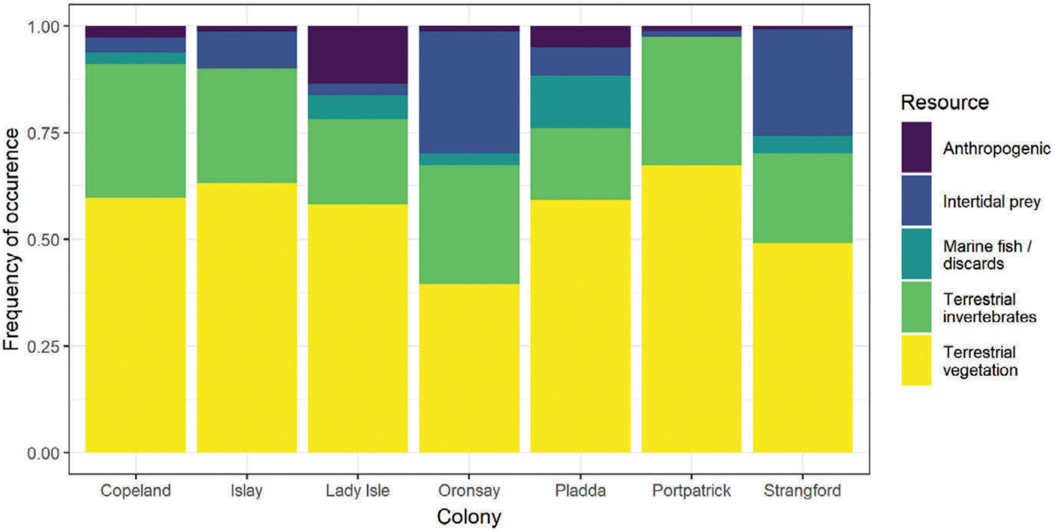

Appendix 1. Frequency of occurrence of Herring Gull *Larus argentatus* pellets containing anthropogenic (likely scavenged from humans, landfill or built-up areas and included processed food as well as plastics and glass indicative of scavenging in these habitats), intertidal prey (including crabs, mussels, sea urchins, marine shells/snails and starfish), marine fish/discards (including *Nephrops* sp.), terrestrial invertebrates and terrestrial vegetation (including grain). The data was combined across years (2013 and 2014) and breeding stages (pre and post hatching) as no differences between years or breeding stages were found.