

Individuality of foraging behaviour in a short-ranging benthic marine predator: incidence and implications

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ABSTRACT: Individual foraging site fidelity (IFSF) has been documented in a wide range of species, but few studies have examined the incidence or implications of variation among individuals in levels of fidelity, especially among short-ranging species where costs of travel place fewer constraints on exploring alternative foraging sites. Using combined GPS and dive data for 560 trips by 70 birds, we quantified the repeatability of foraging behaviour including IFSF in a short-ranging, mainly benthic predator, the European shag *Phalacrocorax aristotelis*, across 3 consecutive breeding seasons at a colony in NE England. There was significant repeatability in a wide range of foraging trip parameters, with highest consistency in those related to foraging location and maximum dive depth, and lowest consistency in those related to trip duration and time spent in different activities. Birds also had high IFSF overall but there was marked variation among individuals in this respect: some were highly consistent in the locations visited over multiple years whereas others frequently changed their foraging locations between successive trips. IFSF was typically higher from one year to the next than within a single year, with most birds retaining similar levels of consistency from year to year. Females with higher IFSF during chick-rearing were in better condition than birds with lower consistency and had earlier hatching dates. These data strongly suggest IFSF may be beneficial even in short-ranging species, at least in benthic feeders where prior knowledge and experience of particular habitat patches and associated prey capture techniques may be advantageous.

KEY WORDS: Individual foraging site fidelity · Individual difference · GPS tracking · Site familiarity · European shag · *Phalacrocorax aristotelis* · Benthic predator · Diving behaviour

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1. INTRODUCTION

Foraging behaviour is a key component in the daily routines of many species and forms a vital link between prey availability, predator reproductive success and fitness. There is increasing realization that in many animal populations, foraging behaviour differs consistently among phenotypically similar individuals, with far-reaching implications for ecology, evolution and wildlife management (Bolnick et al. 2003, Piper 2011, Wakefield et al. 2015). One com-

mon form of consistency is individual foraging site fidelity (IFSF), where an individual repeatedly uses the same foraging location on successive foraging trips. IFSF has been recorded in marine birds (Irons 1998, Hamer et al. 2001, Weimerskirch 2007) and other colonial central-place foragers such as pinnipeds (Bradshaw et al. 2004, Baylis et al. 2012, Arthur et al. 2015), bats (Kerth et al. 2001, Hillen et al. 2009) and ants (Beverly et al. 2009). IFSF could arise as a result of fitness advantages associated with increased foraging efficiency, achieved by learning

and remembering the location of consistently productive foraging sites (Votier et al. 2017, Grecian et al. 2018). For instance, Patrick & Weimerskirch (2017) recorded that IFSF was linked to higher breeding success in black-browed albatrosses *Thalassarche melanophris* both within a single breeding season and across years. However, the processes generating and maintaining IFSF are not well understood, and only recently have studies started to explore the variation within or between populations in levels of individual consistency in foraging movements and behaviour (Patrick et al. 2014, Potier et al. 2015, see review by Phillips et al. 2017).

Previous studies of IFSF have focussed primarily on mid- to long-ranging marine predators, which may spend several consecutive days away from their breeding sites, travelling hundreds to thousands of kilometres to provide food for their offspring (Call et al. 2008, Wakefield et al. 2015, Patrick & Weimerskirch 2017). For these species, knowing where profitable foraging areas are likely to occur could greatly reduce the time and energy costs of locating prey. In contrast, such costs may be much lower for short-ranging species, providing a greater potential benefit of exploring alternative foraging sites. However, recent studies have recorded repeatability in foraging behaviour in species with relatively short foraging ranges (<30 km), leading to calls for further studies of individual repeatability in short-ranging species (Kotzerka et al. 2011, Harris et al. 2014, Potier et al. 2015).

European shags *Phalacrocorax aristotelis* (hereafter shags) are coastal foragers with a very short for-

aging range (median = 3.4 km, interquartile range = 1.6–7.5 km; Wakefield et al. 2017). They feed mainly at the seabed but can also exploit pelagic prey (Watanuki et al. 2008, Howells et al. 2017). During the breeding season, adults make 3–4 foraging trips d^{-1} on average (Wanless et al. 1993) and at certain sites, birds may nest within sight of conspecifics foraging, and so could potentially assess patch quality even before leaving the colony (Evans et al. 2016). During benthic and demersal foraging, however, it may be difficult for birds to assess prey availability before initiating a dive other than through prior experience. Here we examined the repeatability in the foraging behaviour of shags over different time scales, and we explore the relationships between variation in the level of IFSF shown by individuals and different putative measures of foraging success and fitness.

2. MATERIALS AND METHODS

2.1. Study site and data collection

Fieldwork was conducted at the Farne Islands, UK (55° 36' 57.30" N, 1° 39' 20.19" W) in May to July of 3 years (2014 to 2016). Catching effort was focussed at 3 sites within the archipelago (Fig. 1): 1 at Inner Farne in the inner group of islands (ca. 2 km from the mainland) and 2 in the outer group (ca. 5 km offshore). Each year, birds attending 2–4 wk old chicks were caught at the nest using a noose, crook or by hand, sexed (males were distinguished from females

by larger size and croaking call; Baker 1993, Grist et al. 2017), weighed (to the nearest gram using a digital balance) and (if not already ringed) each bird was fitted with a metal British Trust for Ornithology ring and an individually numbered plastic colour ring.

GPS loggers (IgotU GT-120, Mobile Action Technology) and time-depth recorders (TDRs: G5, CEFAS Technology) were combined into a single device using shrink wrap, cable ties and Tesa® tape, then taped to the underside of the central tail feathers. Loggers were programmed to collect fixes every minute, with TDRs set to take readings at regular intervals (once per hour in 2014, every 20 min in 2015 and 2016) throughout the day and at maximum resolution (12 Hz in 2014, 2 Hz in 2015 and 2016) when submerged

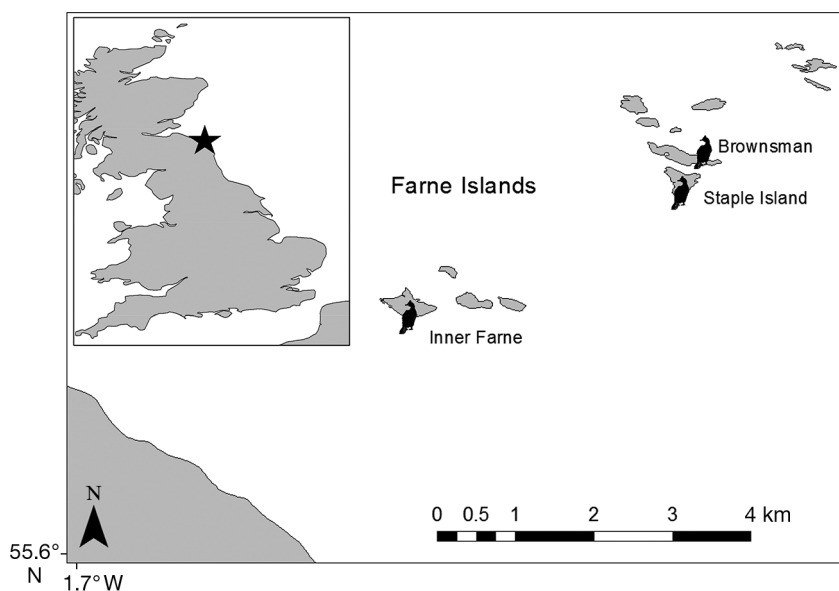


Fig. 1. Locations of breeding colonies (shag icons) in the Farne Islands where European shags were tracked. Inset shows location of the Farne Islands within the UK

below 1.5 m. Birds were re-captured after 4 to 5 d to remove devices, re-weighed (as above) and measured (maximum wing chord to the nearest millimetre using an end-stopped rule, bill depth to the nearest millimetre using digital callipers) before release to the nest. The combined weight of the loggers (34 g) was <2% of average body weight and well within the recommended 3% guideline (Phillips et al. 2003). Similar devices have been deployed on shags in a number of recent studies with no reported adverse effects (Fortin et al. 2013, Soanes et al. 2014, Wakefield et al. 2017), and we found no significant change in body masses of tagged birds between deployment and retrieval (paired *t*-test: $p = 0.08$) and no differences were apparent in trip durations of tagged birds and untagged controls.

2.2. Data processing

GPS data were interpolated to 60 s to account for missing and duplicate locations recorded by the loggers. Dive data were zero offset corrected to periods when birds were at the surface (identified from dive profiles), and dive parameters were extracted using the package DiveMove (R version: R v 3.1.2) (Luque & Fried 2011). Calibrated dive data were then merged with locational data by matching date and time values to the nearest 60 s. Based on visual inspections of data, potential foraging trips were defined as successive locations where a bird spent over 30 min away from the colony and that also included at least 1 bout of diving activity to a depth >1.5 m (the depth at which TDRs were triggered, confirming the bird had landed on the water). Shags often spend time at the colony but away from the nest (Grémillet et al. 1998). As such, in order to encompass all 'dry points' of each island, we used a distance of 200 m from the central point of each island as the limit of each colony. This ensured that occasions when birds left the nest but stayed on land were excluded, while allowing the inclusion of data for locations at sea close to the colony.

Behavioural states were assigned to each location during foraging trips using GPS and TDR data. To achieve this, the speed between successive locations was calculated from GPS distance and time data. Ground speeds between 4 and 30 m s⁻¹ were classified as flight (data from Pennycuik 1987, extended as suggested by Kogure et al. 2016). Speeds of <2 m s⁻¹ were classified as resting or diving on the basis of TDR data. Dives ≥5 m were classified as foraging dives, with shallower dives being associated with

washing and surface swimming (Watanuki et al. 2008). Trips that did not include any foraging dives were then excluded from further analyses. Resting activity was subdivided into resting on land (depth at high-water ≤0 m) and resting at sea (depth at high-water >0 m). A small number of speeds (ca. 2% of the total) were between 2 and 4 m s⁻¹, mainly during take-off and landing, and these behavioural events were excluded from the analysis.

2.3. Individual consistency

To describe the distribution and consistency of individual foraging effort, we calculated the following variables for each foraging trip: (1) duration in minutes (the time elapsed between a bird crossing the 200 m threshold and returning to within 200 m of the colony); (2) total distance travelled in km, as above; (3) departure angle in degrees (calculated by averaging the first 10 bearings that were >50 m from the colony); and (4) foraging range in km (greatest distance attained from the colony). For trips where TDR and GPS data could be matched, we also calculated: (5) mean longitude and (6) mean latitude of dive locations in each trip; (7) mean depth in m at the bottom of each dive; (8) proportion of time spent in dives per trip (calculated as the percentage of 60 s intervals with depth ≥5 m); (9) total time spent at the bottom phase of dives per trip (indicative of time spent probing for or pursuing prey); and (10) proportion of time spent resting per trip (calculated as the percentage of 60 s intervals with speed <2 m s⁻¹ and depth <5 m, which included both pauses at the sea surface between dives and occasions when birds rested on land away from the colony during a trip).

On a small number of occasions, TDRs malfunctioned, resulting in no dive depths being recorded for all or part of a trip. As shags are unlikely to spend time resting on water when they are not foraging (Daunt et al. 2007), on these occasions it was assumed that periods of repeated slow speeds (<2 m s⁻¹) at distance >200 m from the colony were associated with diving activity, as was the case for all trips with complete GPS and TDR data. These trips with partial data were included in the analysis of trip durations, distances and dive locations, but in no other analysis. Birds roosted on land away from the colony overnight on a few occasions ($n = 8$), and these were removed from the trip analyses. One nest failed during the tracking period in 2015, probably due to predation of the brood, and all of this bird's data were also removed from analyses.

For each trip parameter except angle of departure, we calculated repeatability (r) values and their associated standard errors and p -values based on the ratio of between-group and within-group variance components from a GLMM structure, using the R package 'rptR' v.0.6.405 (Nakagawa & Schielzeth 2010). As bearings are circular measures bounded by 0 and 360°, for angle of departure we used a circular ANOVA (R package 'circular' v.0.4-7; Agostinelli & Lund 2013) and calculated repeatability and associated standard error using Lessells & Boag (1987) and Becker (1984; p -values are not available using this method).

In addition to examining the trip parameters above, we also used the R package 'adehabitat' v.0.4.13 (Calenge 2006) to examine the consistency in foraging locations used by individual birds. For this analysis we calculated a utilization distribution (UD) for every foraging trip each year using only locations classified as diving activity. The choice of smoothing parameter (h) used in these calculations can greatly influence the results obtained (Worton 1989). Hence, in order to choose a biologically relevant h -value, minimum convex polygons (MCPs) were calculated for each bird to obtain the mean area used within a single trip. The radius of a circle with the area of the mean MCP was then calculated and used as the smoothing parameter. We then generated 95% UD, indicating the area used for foraging during each trip (Wakefield et al. 2015), using bivariate normal kernels with a fixed bandwidth (h) of 340 m over a 0.1×0.1 km grid. To examine IFSF, we next used Bhat-tacharyya's affinity (BA; Fieberg & Kochanny 2005) to quantify the pairwise overlap in the 95% UD of trips by each individual each year. BA gives a measure of spatial similarity, with scores bounded between 0 (no overlap, i.e. no spatial consistency) and 1 (complete overlap, i.e. perfect spatial consistency). We recorded a mean of 8 trips (equating to 2–3 d of foraging effort) $\text{bird}^{-1} \text{yr}^{-1}$. Therefore, to standardise sample sizes for this analysis, we used only the first 8 trips birds made. To test whether IFSF each year was greater than expected by chance, we used a randomisation procedure to generate a null distribution, with bird identity randomly re-assigned to trips for 100 permutations each year (following Wakefield et al. 2015).

2.4. Potential fitness consequences

To investigate whether individuals with stronger IFSF had a potential fitness advantage over less con-

sistent birds, we examined the relationships between within-year BA scores and adult body condition (higher condition associated with higher annual survival and reproductive success, e.g. van Noordwijk & de Jong 1986, Milenkaya et al. 2015) and timing of breeding (earlier laying associated with higher breeding success; Daunt et al. 2006). An index of body condition was calculated for all tracked birds using the residuals from an ordinary least squares linear regression of adult body mass against wing length. This method has been found across a range of species to provide a useful indication of individuals' energy reserves (Labocha & Hayes 2012), especially in species where there is a strong relationship between body mass and fat mass (Jacobs et al. 2012), which includes shags (Labocha & Hayes 2012). Nonetheless, because the relationship between body mass and length changes as body size changes, such condition indices may produce spurious differences (e.g. between sexes) that are simply a consequence of differences in body size (Peig & Green 2010). We avoided this problem by calculating and analysing values for each sex separately (there was no indication of a non-linear relationship between body mass and wing length in either sex). We also used the earliest hatching date within each brood (recorded at Inner Farne only, by daily observation of nests) to indicate timing of laying by females. To account for differences between years, hatching dates were standardised by calculating the difference in days from the earliest recorded hatching date each year.

We constructed generalised linear mixed models (GLMMs) within the R package 'lme4' v.1.1-7 (Bates et al. 2015) to examine how adult body condition and females' timing of breeding were related to IFSF while controlling for other effects. Separate models of body condition were constructed for males and females to avoid pseudoreplication of data at nests where both partners were tracked. All models included year as a fixed effect and bird identity as a random effect to account for individuals tracked in >1 year. Models of body condition also included sub-colony (Inner Farne or outer group) as a fixed effect. To test if within-season IFSF differed between years, sexes or sub-colonies, an additional GLMM was constructed with year, sex and sub-colony as fixed effects and bird identity as a random effect. Fixed effects were standardised using the 'arm' package v.1.7-07 (Gelman & Su 2014) to ensure they were on a common scale and to increase the interpretability of parameter estimates (Schielzeth 2010).

Model simplification and selection were performed using a multi-model inference approach based on the

methods and recommendations of Grueber et al. (2011), using the 'MuMIn' package v.1.13.4 (Bartoń 2015). A set of candidate models was first identified for each response variable, with all possible subsets of predictor variables and interactions considered. Support for different candidate models was then assessed using Akaike's information criterion adjusted for small sample size (AICc) and Akaike weights. Model sets representing the 95% confidence intervals of the summed weights were selected, and parameter estimates and the relative importance of each parameter were then averaged across selected models (Burnham & Anderson 2002), with test statistics and p-values extracted using the package 'LMERConvenienceFunctions' (Tremblay & Ransijn 2015).

3. RESULTS

We tracked 70 birds (52 unique individuals; 29 males and 23 females) over the 3 yr study with combined TDR and GPS data for 66 birds (51 unique individuals; 28 males and 23 females). Multiple foraging trips were recorded for most birds (mean = 8 trips bird⁻¹, range = 1–21) and 11 individuals were tracked

over 2 or more breeding seasons and had sufficient data for analyses. Over the study period, 8 pairs were tracked either simultaneously (n = 4) or consecutively (n = 4) within the same season. Birds foraged up to 4.5 km from their nests, most of which were within 2 km of each other.

3.1. Individual consistency and foraging site fidelity

There was significant repeatability in a wide range of foraging trip parameters of individual birds each year, with the highest consistency in parameters related to foraging location and maximum dive depth, and lowest consistency in parameters related to trip duration and time spent in different activities (Table 1). In addition, the observed overlap in the UD's of successive trips by individual birds (BA score) each year was much greater than expected by chance in each of the 3 study years (Table 2), indicating a high level of IFSF. However, we found marked variation among individuals in this respect (Fig. 2), with individual BA scores ranging from 0.06 to 0.75 (Table 2; mean \pm SD = 0.32 \pm 0.18). There was no significant difference in BA scores between years ($z = 0.16$, CI = -0.09 to 0.08, $p = 0.87$), sexes ($z = 0.67$, CI = -0.12 to

Table 1. Summary of different foraging behaviour variables and their associated repeatability estimates for European shags raising chicks at the Farne Islands, UK. Variables are ranked from highest to lowest repeatability values (r), shown together with 95% confidence intervals and p-values for tests of significant repeatability (except for angle of departure). NA: not assessed

Trip parameter	n (trips)	Foraging behaviour			Repeatability estimates		
		Mean	SD	Range	r	95% CI	p
Mean longitude of dives ($^{\circ}$ W)	775	1.65	0.05	1.80 to 1.54	0.665	0.559–0.749	<0.01
Mean depth at bottom of dive (m)	708	19.57	8.03	2.44–44.02	0.639	0.522–0.726	<0.001
Angle of departure from colony ($^{\circ}$)	775	201.09	82.26	2.60–358.30	0.563	0.460–0.667	NA
Proportion of time resting	708	0.41	0.16	0.00–0.96	0.554	0.438–0.643	<0.001
Mean latitude of dives ($^{\circ}$ N)	775	55.62	0.02	55.49–55.71	0.515	0.403–0.611	<0.01
Maximum distance from colony (km)	775	3.16	2.20	0.10–14.11	0.448	0.331–0.544	<0.001
Total distance travelled (km)	775	6.66	4.78	0.01–29.40	0.430	0.311–0.526	<0.001
Proportion of time in dives	708	0.43	0.16	0.02–0.86	0.369	0.253–0.470	<0.001
Total time at bottom of dives (min)	708	22.09	13.41	1.02–114.50	0.333	0.225–0.435	<0.001
Trip duration (min)	775	86.80	42.66	22.00–290.00	0.304	0.197–0.402	<0.001

Table 2. Spatial consistency estimates (Bhattacharyya's affinity [BA] scores) for 95% utilization distributions (UD's) of dives made during successive foraging trips by individual shags, together with null estimates indicating the mean overlap expected by chance, in 3 consecutive breeding seasons. Significant (p) values from a Wilcoxon rank sum test between null permutations and observed BA scores are also shown for each year

Year	n (individuals)	Mean overlap in UD's (range)	Null expected overlap in UD's (range)	p
2014	26	0.330 (0.113–0.742)	0.016 (0.013–0.020)	<0.001
2015	20	0.326 (0.093–0.751)	0.016 (0.012–0.020)	<0.001
2016	12	0.301 (0.060–0.687)	0.007 (0.005–0.009)	<0.001

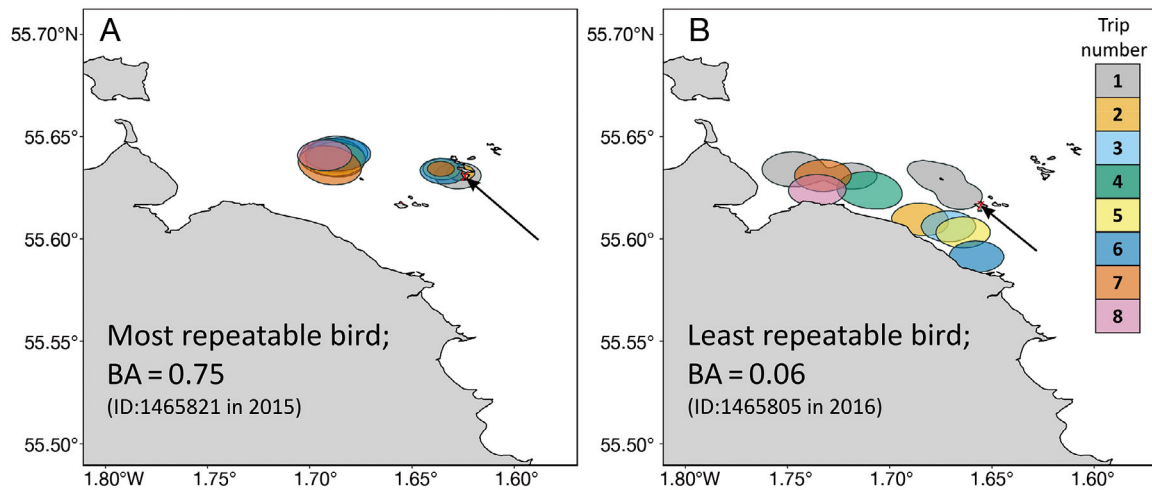


Fig. 2. Foraging areas used in successive trips by (A) the most repeatable European shag in the dataset and (B) the least repeatable bird. Colours represent 95 % utilization distributions (UDs) of locations of dives during each trip. BA score is the mean Bhattacharyya's affinity (see Section 2. for further explanation). Red crosses (indicated by arrows) show breeding sites of tagged birds

0.06, $p = 0.50$) or island groups ($z = 1.49$, $CI = -0.02$ to 0.16 , $p = 0.14$).

We tracked 11 birds in more than 1 year, and these showed marked variation in the extent to which individuals exploited the same foraging areas in different years, with BA scores of individuals across years ranging from 0.02 to 0.82 (Fig. 3). Nine birds (82 %) showed greater foraging site fidelity (i.e. higher BA scores) between years than within (Fig. 4), indicating that individuals tended to exploit the same range of foraging areas in different years even if they had relatively low IFSF in any given year.

3.2. Potential fitness consequences of IFSF

Females with higher IFSF bred earlier than those with lower IFSF: BA score was the only predictor variable contained in the top model set for hatching date (Table 3), showing a significant negative relationship (Fig. 5; $F_{1,12} = 8.35$, conservative p -value = 0.01). Females with higher IFSF were also in better condition during chick-rearing (Fig. 5): IFSF was the strongest-weighted predictor variable in the best candidate model set for body condition index (Table 4) and had a strong and significant positive

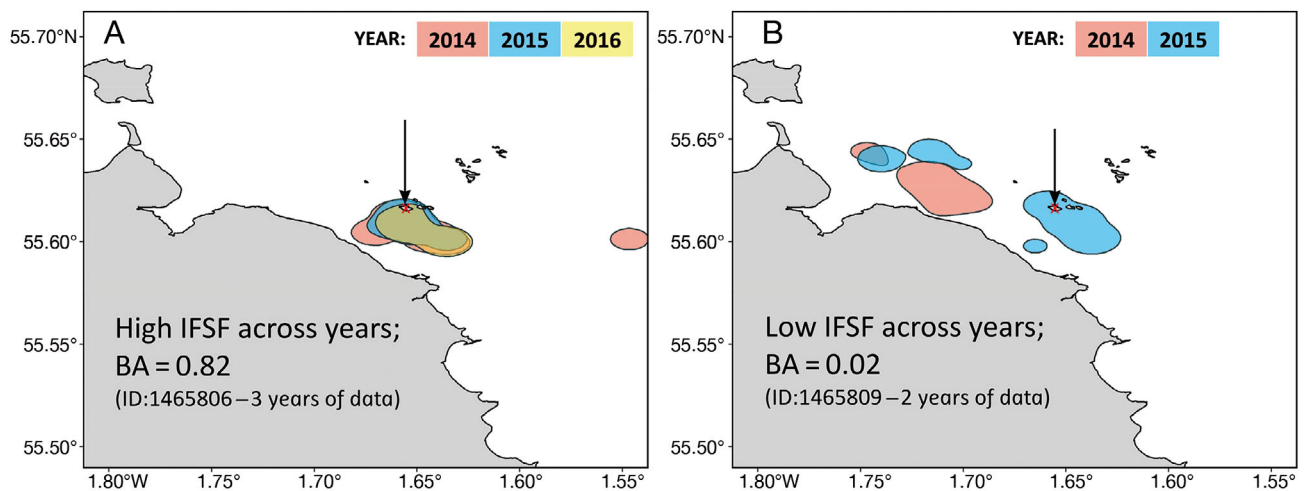


Fig. 3. Foraging areas used in successive breeding seasons by an individual European shag with (A) high and (B) low individual foraging site fidelity (IFSFS) across years. Colours represent 95 % kernel of active foraging areas for each year. BA score is the mean Bhattacharyya's affinity (see Section 2 for further explanation). Red crosses (indicated by arrows) show breeding sites of tagged birds

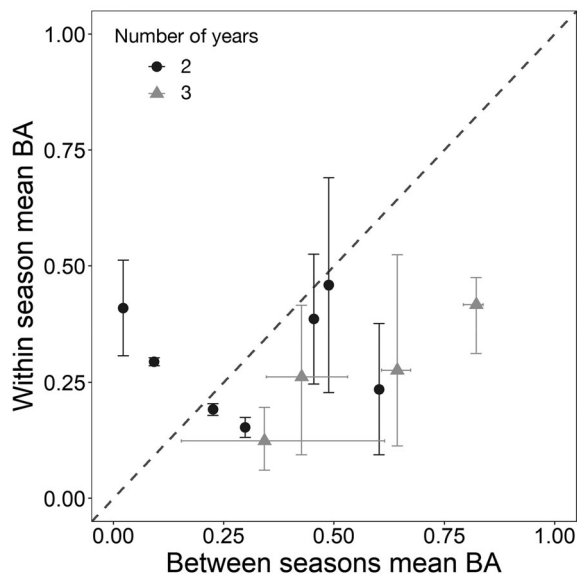


Fig. 4. Relationship between an individual European shag's spatial repeatability score (mean Bhattacharyya's affinity [BA] score) within a single breeding season and between breeding seasons. The dashed line indicates a 1:1 relationship. x-axis error bars show the range of within-season BA scores; y-axis error bars show the range between years

effect averaged across all selected models (Table 4). BA scores of males were not related to their body condition during chick-rearing, but males nesting at Inner Farne had higher condition on average than those at the outer group of islands ($z = 2.14$, $p = 0.03$).

4. DISCUSSION

We found significant IFSF in shags, with all individuals showing greater spatial consistency in their foraging areas than expected by chance. Individuals potentially had access to the same food patches at any given time, yet individuals typically foraged habitually at a restricted number of sites within the overall population-level foraging range. This suggests that IFSF may be beneficial even in short-ranging species where the time and energy costs of visiting alternative foraging locations are relatively low. For shags, this benefit may arise because birds almost exclusively feed close to the seabed, where they forage in 2 distinct habitats (sandy areas with pebbles, shells and occasional brittlestars, and rocky areas with brittlestars, soft coral and kelp), using markedly different foraging behaviour and prey capture techniques in each habitat (Watanuki et al. 2008). Hence, while there was no evidence from our study that individuals specialised in foraging in one or the other habitat, prior knowledge and experience of particular habitat patches and associated prey capture techniques may be advantageous for successful foraging. Benthic habitats also contain numerous static features, potentially enabling foraging birds to memorize topographic cues more easily and improve prey encounter rates (Phillips et al. 2017). Specialisation of this sort may also reduce competition between conspecifics, especially in short-ranging species (Bolnick et al. 2003, Riotte-Lambert et al. 2015).

Table 3. Model selection results for effects of different predictor variables on potential fitness correlates of female and male shags. IFSF: individual foraging site fidelity; logLik: log-likelihood; AICc: Akaike's information criterion corrected for small sample size

Response variable (n individuals)	Rank	Best model(s)	df	logLik	AICc	Δ AICc	Weight
Females							
Body condition (25)	1	IFSF	4	25.87	-41.73	0	0.38
	2	(Null)	3	23.81	-40.49	1.25	0.20
	3	IFSF + Year	5	26.67	-40.17	1.56	0.17
	4	Sub-colony + IFSF	5	26.2	-39.23	2.5	0.11
	5	Sub-colony	4	24.2	-38.41	3.33	0.07
	6	Year	4	24.15	-38.3	3.44	0.07
Hatching date (13)	1	IFSF	4	-48.21	108.86	0	0.73
	2	(Null)	3	-51.28	110.95	2.09	0.26
Males							
Body condition (32)	2	Sub-colony + Year	5	28.51	-44.72	1.57	0.16
	3	(Null)	3	25.54	-44.23	2.06	0.12
	4	Sub-colony + IFSF	5	28.22	-44.13	2.16	0.12
	5	Year	4	26.53	-43.57	2.71	0.09
	6	IFSF + Year	5	27.94	-43.57	2.71	0.09
	7	Year	4	26.46	-43.44	2.84	0.08

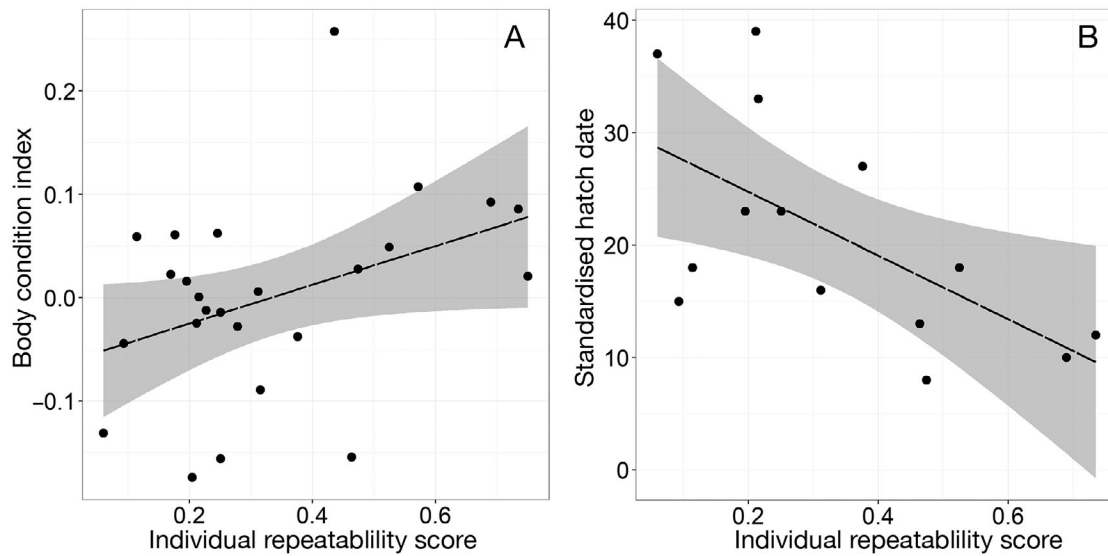


Fig. 5. Relationships between repeatability (individual foraging site fidelity) scores of female European shags and (A) body condition and (B) hatching date. Lines represent linear regressions and shaded areas show 95 % confidence intervals

Table 4. Model-averaged estimates for factors affecting the body condition of female shags (N = 25). N models = 6; IFSF: individual foraging site fidelity; *: significant at $p < 0.05$

Parameters in best model(s)	Estimate	Confidence interval	p	Relative importance
IFSF	0.21	0.01 to 0.15	0.042*	0.66
Year	-0.04	-0.12 to 0.03	0.287	0.24
Sub-colony	0.03	-0.05 to 0.11	0.427	0.18

In addition to foraging locations, individuals also showed high repeatability in maximum dive depths, probably as a consequence of IFSF since most dives were likely to be to the seabed (Watanuki et al. 2008). We also found that angle of departure from the colony was more repeatable than distance travelled per trip, suggesting that birds anticipated overall trip direction but were able to respond opportunistically to proxies for prey availability such as the presence of conspecifics (Grémillet et al. 1999, Hamer et al. 2001, Pettex et al. 2010, Evans et al. 2016). Variables less influenced by location, such as trip duration and time spent in dives and at the bottom of each dive, were less repeatable, as also found in other species, probably reflecting fine-scale variation in prey availability, individual energy requirements or conditions experienced during trips (Patrick et al. 2014, Grecian et al. 2018). Low repeatability in foraging locations and distances travelled by great cormorants *Phalacrocorax carbo* at Chausey, France, was attributed in part to large

tidal fluctuations requiring birds to shift locations across the tidal cycle to forage in similar depth conditions over time (Potier et al. 2015). The tidal range around the Farne Islands (ca. 5 m) is substantially lower than around Chausey (ca. 14 m; Grémillet et al. 1999), which may account for the higher levels of repeatability found in our study.

Previous studies tracking individuals across years have recorded greater levels of consistency in foraging behaviour within a single year than between years (Woo et al. 2008, Harris et al. 2014). In contrast, we found that IFSF was typically higher from one year to the next than within a single year, suggesting that prey availability around the islands was relatively stable across years. Hence, while individuals may have foraged in more than 1 location each year, they tended to use the same range of locations from one year to the next, as also found in northern gannets *Morus bassanus* (Wakefield et al. 2015). Birds were tracked for only a relatively short period during chick-rearing each year, but the fact that they showed as much consistency in foraging areas between years as within any one year suggests that the observed IFSF was not a short-term phenomenon. Levels of behavioural consistency may nonetheless have differed across the breeding cycle with seasonal changes in prey availability (Harris et al. 2014), although in Kerguelen shags *P. verrucosus*, birds instrumented during both incubation and chick-rearing used the same foraging areas, suggesting that individuals showed consistent IFSF over the whole breeding season (Camprasse et al. 2017).

While repeatability of foraging behaviour was high overall, there were nonetheless marked differences among individuals in the degree of IFSF, highlighting the presence of both highly consistent and highly inconsistent individuals within the population, as also found in great cormorants (Potier et al. 2015). Studies of some avian species have suggested that males may have more repeatable behaviour than females (Nakagawa et al. 2007, Ceia et al. 2012), although a meta-analysis of data for 98 species indicated that when mate preference was omitted from the data set, the pattern was reversed and females were more repeatable than males (Bell et al. 2009). Overall we did not find that behavioural consistency differed between sexes (akin to findings in great cormorants; Potier et al. 2015), but previous studies of cormorants and shags have shown females to be more consistent than males in their foraging behaviour (Harris et al. 2013, 2014, Ratcliffe et al. 2013, Camprasse et al. 2017), suggesting that this may be the more typical pattern in this taxon. Differences among individuals in IFSF could have resulted from individuals gradually learning to identify and relocate profitable prey patches, with the level of IFSF reflecting individual age and experience (Riotte-Lambert et al. 2015, Votier et al. 2017, Grecian et al. 2018), although the main difference in this respect appears to be between immatures and adults, and all individuals in our study were breeding adults. Individuals may also differ in the environmental cues used to detect suitable foraging areas while flying over the sea surface (Votier et al. 2010, Patrick & Weimerskirch 2014, Wakefield et al. 2015). Differences in the spatial predictability of these cues could result in variation in levels of IFSF, although such surface cues may be of less importance to species that exploit benthic and demersal prey.

In mid- to long-ranging species, higher IFSF has been linked to higher body condition (Wakefield et al. 2015), greater reproductive success (Patrick & Weimerskirch 2017) and enhanced longevity (Authier et al. 2012). In short-ranging species, where time and energy costs of travel to and from foraging sites are much lower, IFSF may be much less beneficial. However, we found that females with high IFSF during chick-rearing had laid earlier and were in better condition during chick-rearing than those with low IFSF, supporting the suggestion that foraging-site fidelity was associated with enhanced foraging performance. Productivity was not quantified in this study, but earlier laying in shags is strongly associated with both higher breeding success (Daunt et al. 2006) and higher post-fledging survival of offspring

(Harris et al. 1994). Hence our data not only highlight that levels of repeatability in foraging behaviour can differ greatly within a population but also strongly suggest that IFSF may be beneficial even in short-ranging species, at least in benthic feeders where knowledge and experience of particular habitat patches and associated prey capture techniques may be advantageous for successful foraging.

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