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

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Running page head: Shag foraging consistency

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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 three 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, benthic predator, diving behaviour

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 common 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 and 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 focused 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 and 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 forging 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 foraging range (median = 3.4 km, IQR =1.6-7.5 km; Wakefield et al. 2017). They feed mainly at the seabed but can also exploit pelagic prey (Watanuki at al. 2008; Howells et al. 2017). During the breeding season, adults make 3-4 foraging trips per day 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. 2015). 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 examine 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.

Methods

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 three years (2014 to 2016). Catching effort was focused at three sites within the archipelago (Figure 1), one at Inner Farne in the inner group of islands (c. 2 km from the mainland) and two in the outer group (c. 5 km offshore). Each year, birds attending 2-4 week 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, Taipei, Taiwan) and time-depth recorders (TDRs: G5, CEFAS Technology, Lowestoft, UK) were combined into a single device using shrink wrap, cable ties and Tesa® tape (Milton Keynes, UK), 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 minutes in 2015 and 2016) throughout the day and at maximum resolution (12 Hz in 2014, 2 Hz in 2015 and 2016) when submerged below 1.5 m. Birds were re-captured after 4 to 5 days to remove devices, re-weighed (as above) and measured (maximum wing chord 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 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 difference in trip durations of tagged birds and untagged controls and no significant change in body masses of tagged birds between deployment and retrieval ($P \geq 0.1$ in each case).

Data processing

GPS data were interpolated to 60 seconds 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 (Luque & Fried 2011). Calibrated dive data were then merged with locational data by matching date and time values to the nearest 60 seconds.

Based on visual inspections of data, potential foraging trips were defined as successive locations where a bird spent over 30 minutes away from the colony and that also included at least one 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 ms^{-1} and 30 ms^{-1} were classified as flight (data from Pennycuick 1987, extended as suggested by Kogure et al. 2016). Speeds of less than 2 ms^{-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) and resting at sea (depth at high-water > 0). A small number of speeds (~2% of the total) were between 2 and 4 ms^{-1}, mainly during take-off and landing, and these behavioural events were excluded from the analysis.

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 200m threshold and returning to within 200m of the colony); (2) total distance travelled in km, as above; (3) departure angle in degrees (calculated by averaging the first ten 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-second intervals with depth ≥ 5m); (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-second intervals with speed < 2m s-1 and depth <5m. This 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 (< 2m s^{-1}) at distance >200m 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 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% UDs, 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 km × 0.1 km grid. To examine individual foraging site fidelity (IFSF) we next used Bhattacharyya's affinity (BA; Fieberg & Kochanny 2005) to quantify the pairwise overlap in the 95% UDs 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 eight trips (equating to 2-3 days of foraging effort) per bird per year. Therefore, to standardize sample sizes for this analysis, we used only the first eight trips birds made. To test whether or not 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).

Potential fitness consequences

To investigate whether or not individuals with stronger IFSF had a potential fitness advantage over less consistent 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 (OLS) 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 consequences 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).

Results

We tracked 70 birds (52 unique individuals; 29 males and 23 females) over the three-year 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 per bird, range =1-21) and 11 individuals were tracked over two 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. .

Individual consistency and foraging site fidelity

There was significant repeatability in a wide range of foraging trip parameters of individual birds each year, with 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 UDs of successive trips by individual birds (BA score) each year was much greater than expected by chance in each of the three years studied (Table 2), indicating a high level of IFSF. There was, however, marked variation among individuals in this respect (Figure 2), with individual BA scores ranging from 0.06 to 0.75 (Table 2; mean = 0.32, SD ± 0.18). There was no significant difference in BA scores between year (z=0.16, CI -0.09 to 0.08, p= 0.87) sex (z = 0.67, CI -0.12 to 0.06, p=0.50) or island group (z = 1.49, CI -0.02 to 0.16; p = 0.14).

There were 11 birds tracked in more than one 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 (Figure 3). Nine birds (82%) showed greater foraging site fidelity (i.e. higher BA scores) between years than within (Figure 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 one year.

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 (Figure 5; $F_{1,12}$ = 8.35, conservative P value = 0.01). Females with higher IFSF were also in better condition during chick-rearing (Figure 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 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).

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 two 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 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).

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. 2015). 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 P. 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 (c. 5 m) is substantially lower than around Chausey (c. 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 one 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 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.

Author contributions

EM designed and coordinated the study, collected field data, carried out the statistical analysis and drafted the manuscript; CPFR facilitated and assisted with the collection of field data; RMB facilitated collection of field data and biotelemetry devices were deployed under a special methods permit issued to RMB; CH provided statistical advice and helped draft the manuscript; KCH conceived the study, participated in the design of the study, assisted with the collection of field data and helped draft the manuscript. All authors reviewed the manuscript for intellectual content.

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References

Agostinelli C, Lund U (2013) R package 'circular': Circular statistics (version 0.4–7). https://r-forge.r-project.org/projects/circular/

Arthur B, Hindell M, Bester M, Trathan P, Jonsen I, Staniland I, Oosthuizen WC, Wege M, Lea MA (2015) Return customers: foraging site fidelity and the effect of environmental variability in wide-ranging Antarctic fur seals. PLoS One 10: 19

Authier M, Bentaleb I, Ponchon A, Martin C, Guinet C (2012) Foraging fidelity as a recipe for a long life: foraging strategy and longevity in male southern elephant seals. PLoS One 7: 11

Baker K (1993) Identification guide to European non-passerines. British Trust for Ornithology, Thetford

Bartoń K (2015) Mumin: Multi-model inference. R package version 1.15.1. http://cran.rproject.org/package=MuMIn

Bates D, Maechler M, Bolker B, Walker S (2015). Fitting linear mixed-effects models using lme4. J Stat Softw 67: 1-48

Baylis AMM, Page B, McKenzie J, Goldsworthy SD (2012) Individual foraging site fidelity in lactating New Zealand fur seals: continental shelf vs. oceanic habitats. Mar Mamm Sci 28: 276-294

Becker W (1984) Manual of quantitative genetics. 4th edn. Academic Enterprises, Pulhnan WA

Bell AM, Hankison SJ, Laskowski KL (2009) The repeatability of behaviour: a meta-analysis. Anim Behav 77: 771-783

Beverly, BD, McLendon H, Nacu S, Holmes S, Gordon DM (2009) How site fidelity leads to individual differences in the foraging activity of harvester ants. Behav Ecol 20: 633–638

Bodey TW, Cleasby IR, Bell F, Parr N, Schultz A, Votier SC, Bearhop S (2018) A phylogenetically controlled meta-analysis of biologging device effects on birds: deleterious effects and a call for more standardized reporting of study data. Methods Ecol Evol 9: 946-955

Bolnick DI, Svanback R, Fordyce JA, Yang LH, Davis JM, Hulsey CD, Forister ML (2003) The ecology of individuals: incidence and implications of individual specialization. Am Nat 161: 1-28

Bradshaw CJA, Hindell MA, Sumner MD, Michael KJ (2004) Loyalty pays: potential life history consequences of fidelity to marine foraging regions by southern elephant seals. Anim Behav 68: 1349-1360

Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach. 2nd edn. Springer, Berlin

Calenge C (2006) The package “adehabitat” for the r software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197: 516-519

Call KA, Ream RR, Johnson D, Sterling JT, Towell RG (2008) Foraging route tactics and site fidelity of adult female northern fur seal (Callorhinus ursinus) around the Pribilof Islands. Deep Sea Res Part 2 Top Stud Oceanogr 55: 1883–1896

Camprasse EC, Cherel Y, Arnould JPY, Hoskins AJ, Bustamante P, Bost CA (2017) Mate similarity in foraging Kerguelen shags: a combined bio-logging and stable isotope investigation Mar Ecol Prog Ser 578:183-196

Ceia FR, Phillips RA, Ramos JA, Cherel Y, Vieira RP, Richard P, Xavier JC (2012) Short- and long-term consistency in the foraging niche of wandering albatrosses. Mar Biol 159:1581−1591

Daunt F, Afanasyev V, Silk JRD, Wanless S (2006) Extrinsic and intrinsic determinants of winter foraging and breeding phenology in a temperate seabird. Behav Ecol Sociobiol 59: 381-388

Daunt F, Wanless S, Harris MP, Money L, Monaghan P (2007) Older and wiser: improvements in breeding success are linked to better foraging performance in European shags. Funct Ecol 21: 561-567

Fieberg J, Kochanny CO (2005) Quantifying home-range overlap: the importance of the utilization distribution. J Wildl Manage 69: 1346-1359

Fortin M, Bost, C-A, Maes, P, Barbraud C (2013) The demography and ecology of the European shag Phalacrocorax aristotelis in Mor Braz, France. Aquat Living Resour 26: 179–185

Gelman A, Su Y-S (2014) arm: data analysis using regression and multilevel/hierarchical models. http://CRAN.R-project.org/package=arm

Grecian WJ, Lane J, Michelot T, Wade HM, Hamer KC (2018). Understanding the ontogeny of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived oceanography in hidden Markov models. J R Soc Interface 15: 20180084

Grémillet D, Tuschy I, Kierspel M (1998) Body temperature and insulation in diving great cormorants and European shags. Funct Ecol 12: 386-394

Grémillet D, Wilson RP, Storch S, Gary Y (1999) Three-dimensional space utilization by a marine predator. Mar Ecol Prog Ser 183: 263-273

Grist H, Daunt F, Wanless S, Burthe SJ, Newell MA, Harris MP, Reid JM (2017) Reproductive performance of resident and migrant male, females and pairs in a partially migratory bird. J Anim Ecol 86: 1010-1021

Grueber CE, Nakagawa S, Laws RJ, Jamieson IG (2011) Multimodel inference in ecology and evolution: challenges and solutions. J Evol Biol 24: 699-711

Hamer KC, Phillips RA, Hill JK, Wanless S, Wood AG (2001) Contrasting foraging strategies of gannets Morus bassanus at two North Atlantic colonies: foraging trip duration and foraging area fidelity. Mar Ecol Prog Ser 224: 283-290

Harris MP, Buckland ST, Russell SM, Wanless S (1994) Post-fledging survival to breeding age of Shags Phalacrocorax aristotelis in relation to year, date of fledging and brood size. J Avian Biol 25: 268-274

Harris S, Raya Rey A, Phillips RA, Quintana F (2013) Sexual segregation in timing of foraging by imperial shags (Phalacrocorax atriceps): Is it always ladies first? Mar Biol 160:1249−1258

Harris S, Rey AR, Zavalaga C, Quintana F (2014) Strong temporal consistency in the individual foraging behaviour of imperial shags Phalacrocorax atriceps. Ibis 156: 523-533

Hillen J, Kiefer A, Veith M (2009) Foraging site fidelity shapes the spatial organization of a population of female western barbastelle bats. Biol Conserv 142: 817–823

Howells RJ, Burthe SJ, Green JA, Harris MP and others (2017) From days to decades: short- and long-term variation in environmental conditions affect offspring diet composition of a marine top predator. Mar Ecol Prog Ser 583: 227-242Irons DB (1998) Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding.

Ecology 79: 647-655

Jacobs SR, Elliott K, Guigueno MF, Gaston AJ, Redman P, Speakman JR, Weber J-M (2012) Determining seabird body condition using nonlethal measures. Physiol Biochem Zool 85: 85-95

Kerth G, Wagner M, Konig B (2001) Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (Myotis bechsteini). Behav Ecol Sociobiol 50: 283–291.

Kogure Y, Sato K, Watanuki Y, Wanless S, Daunt F (2016) European shags optimize their flight behavior according to wind conditions. J Exp Biol 219: 311-318

Kotzerka J, Hatch SA, Garthe S (2011) Evidence for foraging-site fidelity and individual foraging behavior of pelagic cormorants rearing chicks in the Gulf of Alaska. Condor 113: 80-88Labocha MK, Hayes JP (2012) Morphometric indices of body condition in birds: a review. J Ornithol 153: 1-22

Lessells CM, Boag PT (1987) Unrepeatable repeatabilities - a common mistake. Auk 104: 116-121

Luque SP, Fried R (2011) Recursive filtering for zero offset correction of diving depth time series with GNU R package diveMove. PLoS One 6:9

Lynch TP, Alderman R, Hobday AJ (2015) A high-resolution panorama camera system for monitoring colony-wide seabird nesting behaviour. Methods Ecol Evol 6: 491-499

Milenkaya O, Catlin DH, Legge S, Walters JR (2015) Body condition indices predict reproductive success but not survival in a sedentary, tropical bird. PLoS One 10: 8 e0136582

Nakagawa S, Gillespie DOS, Hatchwell BJ, Burke T (2007) Predictable males and unpredictable females: sex difference in repeatability of parental care in a wild bird population. J Evol Biol 20: 1674-1681

Nakagawa S, Schielzeth H (2010) Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol Rev 85: 935-956

Patrick SC, Bearhop S, Gremillet D, Lescroel A, Grecian WJ, Bodey TW, Hamer KC, Wakefield E, Le Nuz M, Votier SC (2014) Individual differences in searching behaviour and spatial foraging consistency in a central place marine predator. Oikos 123: 33-40

Patrick SC, Weimerskirch H (2014) Consistency pays: sex differences and fitness consequences of behavioural specialization in a wide-ranging seabird. Biol Lett 10: 0140630

Patrick SC, Weimerskirch H (2017) Reproductive success is driven by local site fidelity despite stronger specialisation by individuals for large-scale habitat preference. J Anim Ecol 86: 674-682

Peig J, Green AJ (2010) The paradigm of body condition: a critical reappraisal of current methods based on mass and length. Funct Ecol 24: 1323-1332

Pennycuick CJ (1987) Flight of Auks Alcidea) and other northern seabirds compared with southern Procellariiformes – ornithodolite observations. J Exp Biol 128: 335-347

Pettex E, Bonadonna F, Enstipp MR, Siorat F, Grémillet D (2010) Northern gannets anticipate the spatioetemporal occurrence of their prey. J Exp Biol 213: 2365-2371

Phillips RA, Jose CX, Croxall JP (2003) Effects of satellite transmitters on albatrosses and petrels. Auk 120: 1082-1090

Phillips RA, Lewis S, Gonzales-Solis J, Daunt F (2017) Causes and consequences of individual variability and specialization in foraging and migration strategies of seabirds. Mar Ecol Prog Ser 578: 117-150

Piper WH (2011) Making habitat selection more "familiar": a review. Behav Ecol Sociobiol 65:1329-1351

Potier S, Carpentier A, Gremillet D, Leroy B, Lescroel A (2015) Individual repeatability of foraging behaviour in a marine predator, the great cormorant, Phalacrocorax carbo. Anim Behav 103: 83-90

Ratcliffe N, Takahashi A, O'Sullivan C, Adlard S, Trathan PN, Harris MP, Wanless S (2013) The roles of sex, mass and individual specialisation in partitioning foraging-depth niches of a pursuit-diving predator. PLoS One 8:e79107

Riotte-Lambert L, Benhamou S, Chamaille-Jammes S (2015) How memory-based movement leads to nonterritorial spatial segregation. Am Nat 185: E103-E116

Schielzeth H (2010) Simple means to improve the interpretability of regression coefficients. Methods Ecol Evol 1: 103-113

Soanes LM, Arnould JPY, Dodd SG, Milligan G, Green JA (2014) Factors affecting the foraging behaviour of the European shag: implications for seabird tracking studies. Mar Biol 161:1335–1348

Tremblay A, Ransijn J (2015) Lmer convenience functions: model selection and post-hoc analysis for (g)lmer models. R package version 2.10

van Noordwijk AJ, de Jong G (1986) Acquisition and allocation of resources: their influence on variation in life history tactics. Am Nat 128:137–142

Votier S, Fayet A, Bearhop S, Bodey T, Clark B, Grecian W, Guilford T, Hamer K, Jeglinski J, Morgan G, Wakefield E, Patrick SC (2017) Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. Proc R Soc B 284: 20171068

Votier SC, Bearhop S, Witt MJ, Inger R, Thompson D, Newton J (2010) Individual responses of seabirds to commercial fisheries revealed using gps tracking, stable isotopes and vessel monitoring systems. J Appl Ecol 47: 487-497

Wakefield ED, Cleasby IR, Bearhop S, Bodey TW, Davies RD, Miller PI, Newton J, Votier SC, Hamer KC (2015) Long-term individual foraging site fidelity: why some gannets don't change their spots. Ecology 96: 3058-3074

Wakefield ED, Owen E, Baer J, Carroll MJ, Daunt F, Dodd SG, Green JA, Guilford T, Mavor RA, Miller PI, Newell MA, Newton SF, Robertson GS, Shoji A, Soanes LM, Votier SC, Wanless S, Bolton M (2017) Breeding density, fine-scale tracking and large-scale modeling reveal the regional distribution of four seabird species. Ecol Appl 27: 2074-2091

Wanless S, Corfield T, Harris MP, Buckland ST, Morris JA (1993) Diving behaviour of the shag Phalacrocorax aristotelis (Aves: Pelecaniformes) in relation to water depth and prey size. J Zool 231: 11-25

Watanuki Y, Daunt F, Takahashi A, Newei M, Wanless S, Sat K, Miyazaki N (2008) Microhabitat use and prey capture of a bottom-feeding top predator, the European shag, shown by camera loggers. Mar Ecol Progs Ser 356: 283-293

Weimerskirch H (2007) Are seabirds foraging for unpredictable resources? Deep Sea Res Part 2 Top Stud Oceanogr 54: 211-223 Woo KJ, Elliott KH, Davidson M, Gaston AJ, Davoren GK (2008) Individual specialization in diet by a generalist marine predator reflects specialization in foraging behaviour. J Anim Ecol 77: 1082-1091

Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. Ecology 70: 164-168

Table 1. Summary of different foraging behaviour variables and their associated repeatability estimates for 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).

	Foraging behaviour				**Repeatability estimates**		
Trip parameter	**n (trips)**	**mean**	**SD**	**range**	**r**	**95% CI**	**P**
Mean longitude of dives	775	-1.65	0.05	-1.80 - -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	<0.01*
Angle of departure from colony	775	201.09	82.26	2.60 - 358.30	0.563	0.460-0.667	N/A
Proportion of time resting	708	0.41	0.16	0.00 - 0.96	0.554	0.438-0.643	<0.01*
Mean latitude of dives	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	<0.01*
Total distance travelled (km)	775	6.66	4.78	0.01 - 29.40	0.430	0.311-0.526	<0.01*
Proportion of time in dives	708	0.43	0.16	0.02 - 0.86	0.369	0.253-0.470	<0.01*
Total time at bottom of dives (minutes)	708	22.09	13.41	1.02 - 114.50	0.333	0.225-0.435	<0.01*
Trip duration (minutes)	775	86.80	42.66	22.00 – 290.00	0.304	0.197-0.402	<0.01*

Table 2. Spatial consistency estimates (BA scores) for 95% utilization distributions (UDs) of dives made during successive foraging trips by individual shags, together with null estimates indicating the mean overlap expected by chance, in three consecutive breeding seasons. Significance (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 UDs (range)**	**Null expected overlap in UDs (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

Table 3. Model selection results for effects of different predictor variables on potential fitness correlates of (A) female and (B) male shags.

(A) Females							
Response variable (n individuals)	**Rank**	**Best model(s)**	**df**	**logLik**	**AICc**	**ΔAICc**	**Weight**
Body condition (n = 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 (n = 13)	1	IFSF	4	-48.21	108.86	0	0.73
	2	(Null)	3	-51.28	110.95	2.09	0.26
(B) Males							
Response variable (n individuals)	**Rank**	**Best model(s)**	**df**	**logLik**	**AICc**	**ΔAICc**	**Weight**
Body condition (n = 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

Table 4. Model-averaged estimates for factors affecting the body condition of female shags.

N models	**Parameters in best model(s)**	**Estimate**	**Confidence Interval**	**P value**	**Relative importance**
6	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

N= 25; *indicates significance at $P < 0.05$ level

Figure legends

Figure 1. Locations of breeding colonies in the Farne Islands where birds were tracked. Inset shows location of the Farne Islands within the UK.

Figure 2. Foraging areas used in successive trips by (A) the most repeatable bird in the dataset and (B) the least repeatable bird. Colours represent 95% UDs of locations of dives during each trip. Crosses show breeding sites of tagged birds.

Figure 3. Foraging areas used in successive breeding seasons by an individual with (A) high and (B) low IFSF across years. Colours represent 95% kernel of active foraging areas for each year. BA score is the mean Bhattacharyya's affinity (see Methods for further explanation). Crosses show breeding sites of tagged birds.

Figure 4. The relationship between an individual's spatial repeatability score (mean BA) 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. BA is Bhattacharyya's affinity (see Methods for explanation).

Figure 5. Relationships between repeatability (IFSF) scores of females and (A) body condition and (B) hatching date. Lines represent linear regression trends.

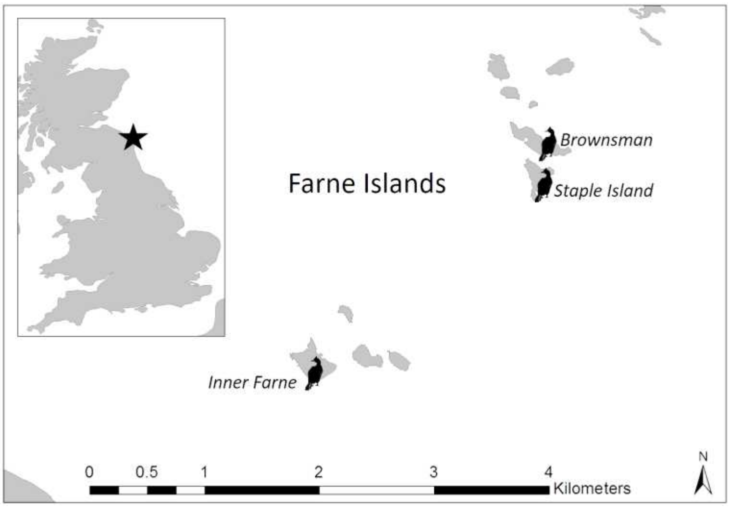
Farne Islands
Brownsman
Staple Island
Inner Farne
0
0.5
1
2
3
4
Kilometers
N

Figure 1

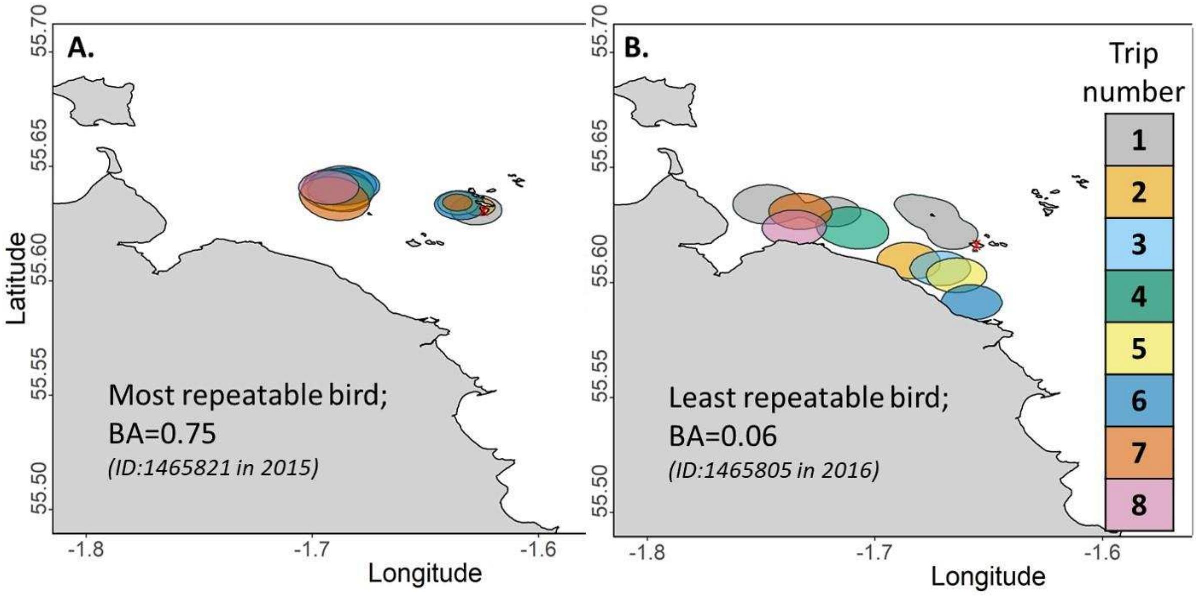
A.
B.
Latitude
55.50
55.55
55.60
55.65
55.70
Longitude
-1.8
-1.7
-1.6
Most repeatable bird;
BA=0.75
(ID:1465821 in 2015)
Least repeatable bird;
BA=0.06
(ID:1465805 in 2016)
Trip number
1
2
3
4
5
6
7
8

Figure 2

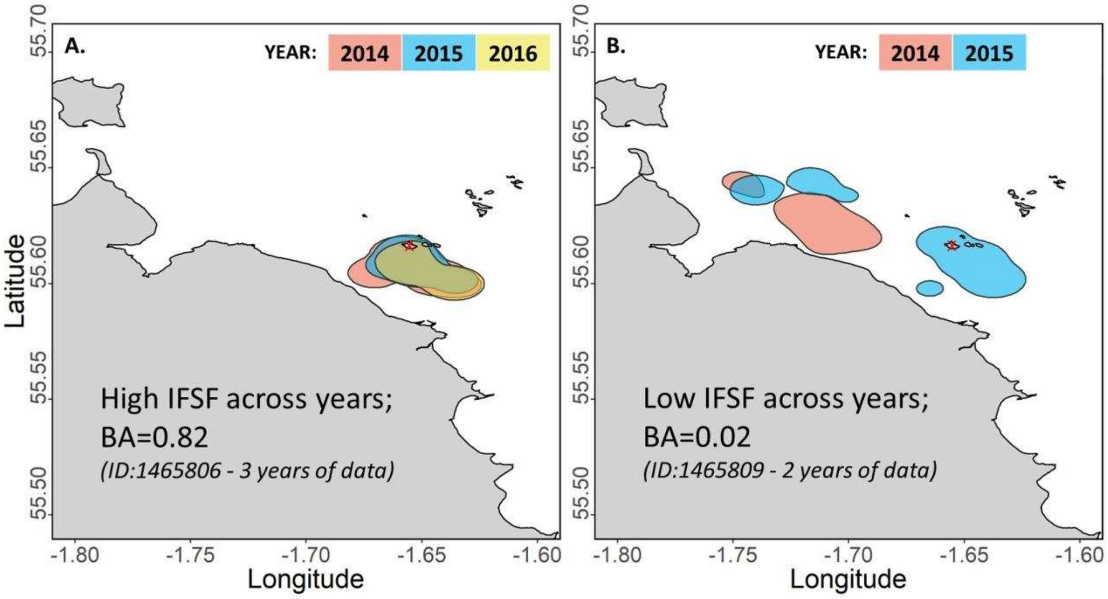
A.
YEAR: 2014 2015 2016
High IFSF across years;
BA=0.82
(ID:1465806 - 3 years of data)
B.
YEAR: 2014 2015
Low IFSF across years;
BA=0.02
(ID:1465809 - 2 years of data)
Latitude
55.50
55.55
55.60
55.65
55.70
Longitude
-1.80
-1.75
-1.70
-1.65
-1.60

Figure 3

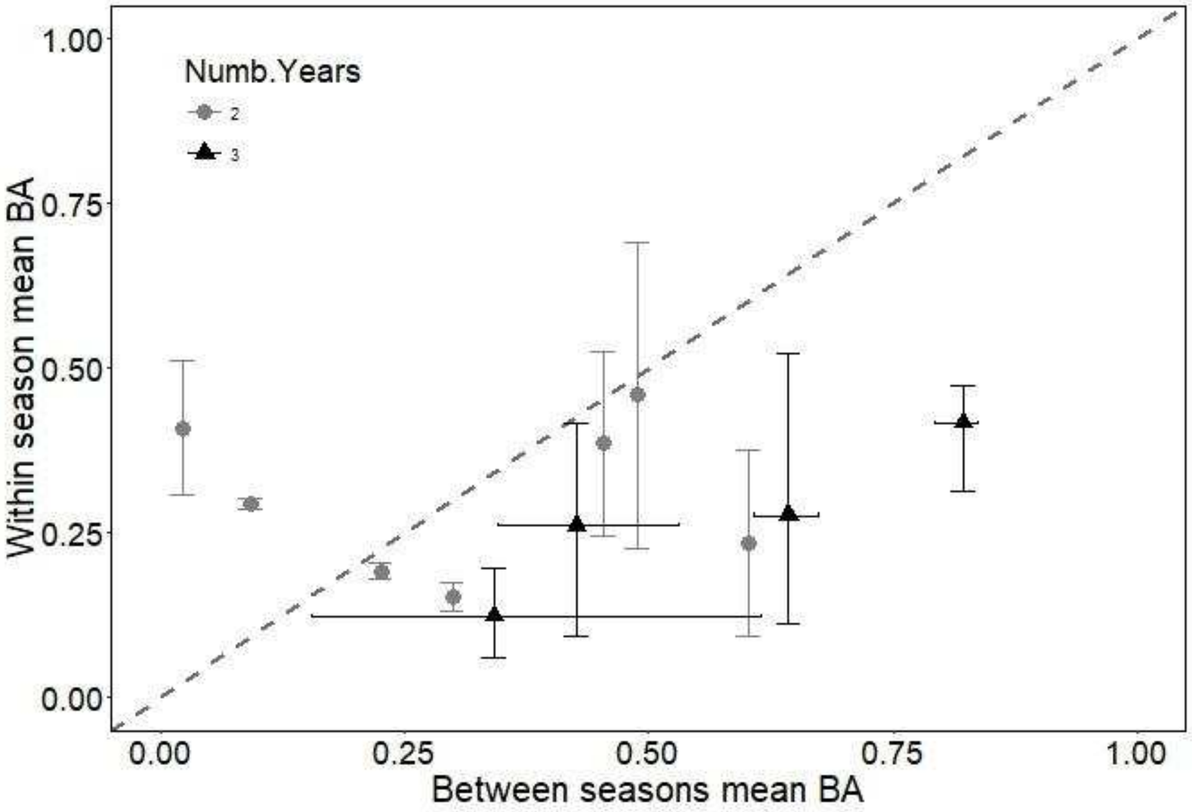
Numb.Years
2
3
Within season mean BA
0.00
0.25
0.50
0.75
1.00
Between seasons mean BA
0.00
0.25
0.50
0.75
1.00

Figure 4

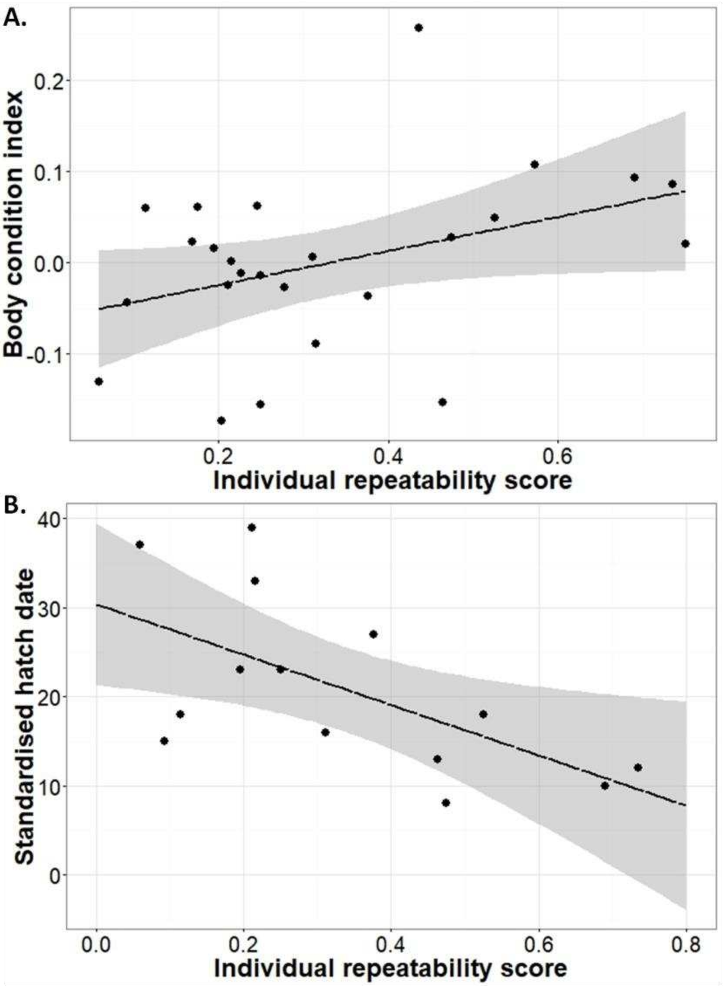
A.
Body condition index
0.2
0.1
0.0
-0.1
0.2
0.4
0.6
Individual repeatability score
B.
Standardised hatch date
40
30
20
10
0
0.0
0.2
0.4
0.6
0.8
Individual repeatability score

Figure 5