

Lower foraging efficiency in immatures drives spatial segregation with breeding adults in a long-lived pelagic seabird

ABSTRACT

Competition, and ultimately adaptive specialisation, are the major ecological forces behind spatial segregation in foraging distributions, and are commonly driven by size-related differences in competitiveness between sex, ages or social status. However such segregation can also be observed in long-lived monomorphic species, often between immature and breeding individuals. These animals often forage in patchy and unpredictable environments where resources can be spread over large scales and difficult to find, and efficient foraging may require advanced cognitive skills (for example in navigation and memory). In these species, experience rather than size may be an important driver of segregation and lead to differences in competitiveness. Here we test this hypothesis by simultaneously tracking individuals at different life stages in a long-lived seabird, the Manx shearwater *Puffinus puffinus*, during a period of central-place foraging around the colony, to investigate spatial segregation, and by measuring foraging efficiency by combining an etho-informatics approach and mass gain. We find substantial spatial segregation between immature and breeding adults, and we find that whilst immatures show a similar foraging effort to adults they have lower foraging success, demonstrating lower foraging efficiency, most likely due to inexperience. Therefore, the deferred breeding observed in shearwaters and many long-lived animals may result from the need to acquire experience in an inherently changeable environment, which may drive intra-specific competition.

23 INTRODUCTION

24 Competition, and ultimately adaptive specialisation, are the major ecological forces behind spatial
25 segregation in foraging distributions, and are commonly driven by size-related differences in
26 competitiveness between sex, ages or social status, in a wide range of animal taxa (e.g. Durant, Kelly,
27 & Caro, 2004; Gosler, 1987; Harcourt, Stewart, & Fossey, 1976; Webb, Marzluff, & Hepinstall-
28 Cymerman, 2012). Long-lived animals with advanced cognitive capacities (vertebrates) may be able
29 to exploit patchy, expansive, and unpredictable environments using individual memory and
30 experience. This could provide a different mechanism driving spatial segregation - even in
31 monomorphic species - if older, more experienced individuals competitively displace younger
32 cohorts through enhanced foraging efficiency. One component of this would be age-related
33 differences in space use correlated with differences in foraging efficiency. Spatial segregation
34 between immature (non-breeding) and breeding adults during all or part of the year occurs in many
35 species (e.g. in primates (Harcourt et al., 1976), other mammals (Cheney & Seyfarth, 1983; Durant et
36 al., 2004; Jarman, 1974), birds (Webb et al., 2012) and insects (Robertson & Cushing, 2011)).
37 Immatures have been found to disperse more and cover greater ranges than breeders, although
38 smaller-scale movements have also been reported (Field, Bradshaw, Burton, Sumner, & Hindell,
39 2005). Understanding such differences is of paramount importance when considering the
40 demography of a species or its conservation needs. It has been suggested that these differences may
41 be due to differences in foraging experience (Lack, 1954), and lower foraging efficiency has been
42 documented in some species (Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; Lefebvre, 1995; Le
43 Vaillant et al., 2012; Maclean, 1986), however the relationship between efficiency and spatial
44 segregation has never been properly tested. Here we investigate this relationship in a long-lived
45 pelagic seabird by tracking simultaneously immature and breeding individuals with a mix of archival
46 and remote-download GPS loggers to investigate potential spatial segregation, while inferring

individual foraging efficiency by combining an etho-informatics analysis of the high-resolution GPS logs to identify different behaviours at sea and estimate foraging effort, and at-colony measurements of foraging success (daily mass gain).

Marine animals, and pelagic seabirds in particular, are often long-lived, with a prolonged immature period, and forage in an open, patchy and unpredictable environment. This may not only give them more opportunities to segregate, but may also make learning and experience particularly important in the development of the skills necessary to forage effectively, e.g. to navigate to distant areas in a featureless environment, to identify and memorise productive areas and often ephemeral prey distributions. This makes them particularly useful model organisms to study stage-related spatial segregation and changes in foraging skills over time; however few studies to date have attempted to do so, mainly because of the logistical challenges involved with tracking non-breeding individuals. Very little is known about the behaviour and distributions of immature pelagic seabirds (Lewison et al., 2012; Shillinger et al., 2012). Studies in penguins, albatrosses and a few large procellariiforms have found that immature seabirds may be more flexible in their destinations and cover a greater spatial range during non-breeding (usually long-scale) movements in the winter (Clarke, Kerry, Fowler, Lawless, & Eberhard, 2003; Kooyman, Kooyman, Horning, & Kooyman, 1996; Kooyman & Ponganis, 2007; Pelletier, Chiaradia, Kato, & Ropert-Coudert, 2014; Peron & Gremillet, 2013; Sherley et al., 2013; Thiebot, Delord, Marteau, & Weimerskirch, 2014; Trebilco, Gales, Baker, Terauds, & Sumner, 2008). However, few have investigated their foraging movements during the breeding season when both adults and immatures act as central-place foragers (Peron & Gremillet, 2013; Riotte-Lambert & Weimerskirch, 2013; Votier, Grecian, Patrick, & Newton, 2011). During this period, stage-related spatial segregation is likely to arise: parental duties force adults to return to the colony regularly because of changes in the cost-benefit trade-offs of different foraging locations. While immatures are not constrained to a colony, they tend to visit their natal colony (or others), generally during a restricted part of the breeding season, to prospect for future nest sites and mates

(Dittmann & Becker, 2003; Harris, 1966; Major & Jones, 2011; C. M. Perrins, Harris, & Britton, 1973). Immature Scopoli's shearwaters *Calonectris diomedea* showed some spatial segregation from breeding adults, but the sample size and resolution of the data are too low to make any strong conclusion (Peron & Gremillet, 2013). Votier and colleagues (2011) showed that immature gannets *Morus bassanus* went further on longer foraging trips and visited other colonies on the way, unlike immature wandering albatrosses *Diomedea exulans* which engaged on shorter trips (in duration and distance) (Riotte-Lambert & Weimerskirch, 2013). However, although both studies suggested that these differences could be a consequence of differences in foraging abilities, they did not test this hypothesis, which is our aim here.

METHODS

Study site and model species

The study was carried out on Skomer Island, Wales (51°44'N, 5°19'W), probably the largest Manx shearwater colony in the world (~300,000 breeding pairs; Perrins et al., 2012), in June-July 2013 and 2014. Manx shearwaters are c. 400g colonial burrow-nesting monomorphic seabirds which mainly breed on the Northeast Atlantic coast. The peak of attendance of immatures at the colony is between mid-June and mid-July (Harris, 1966; Perrins et al., 1973), which coincides with the end of the incubation period and the start of the chick-rearing period. Although hundreds of thousands of immatures visit the colony every year, their at-sea movements and behaviour during this period are currently unknown.

All work was conducted after ethical approval by the British Trust for Ornithology Unconventional Methods Technical Panel (permit C/5311), Natural Resources Wales, Skomer Island Advisory Committee and the University of Oxford.

Deployment of devices

Since immatures appear similar to adults they were identified first by their behaviour on the surface (Brooke, 1990) and then by the absence of a brood patch, having been caught by hand. Breeding adults in study burrows were monitored regularly, via an access hatch, from the start of the breeding season. 50 immature birds (20 in 2013, 30 in 2014), 14 adults at the end of their incubation shift (4 in 2013, 10 in 2014) and 13 chick-rearing adults (2013) were selected for simultaneous device deployment (breeding was later in 2014, therefore all adults were still incubating during the peak of immature attendance at the colony). All birds were weighed and ringed with a metal ring from the British Trust for Ornithology. IgotU GT-120 (Mobile Action Technology Inc., both years) and remote-download Mataki trackers (Mataki.org, 2013) stripped of external casing and waterproofed in heatshrink tubing were configured to record positions every 15min (IgotU) or 60min (Mataki). The latter were also configured to emit a radio signal and look for a download base station every 30min. Devices, made visible with retro-reflective tape for retrieval, were attached to birds' backs using thin strips of marine tape (Tesa 4651 with water-soluble adhesive, see (Guilford, Meade, Freeman, Biro, & Evans, 2008) for details of the methods), and designed to fall off within 2-3 weeks if the bird is not recaptured. Devices (including waterproofing and tape) weighed <19g (IgotU) or <17g (Mataki), which is under 5% of the average total individual body mass. A mix of Mataki and archival GPS loggers were deployed on immatures, while all adults carried an archival logger. Handling time was kept to a minimum (~10min) and birds were released on the colony after deployment.

Retrieval of devices

In the 3 weeks following deployment, 3 observers were posted each night in the capture area, using low intensity red light and night-vision scopes to observe the colony and look for immature study birds. In 2013, 2 remote-download base stations were also installed, each able to detect a radio-signal from any devices within ~200m. Birds seen with a device were caught by the closest observer. In total 20 immatures were recaptured, their device retrieved and data successfully downloaded. At

least 2 more birds were seen but evaded recapture. For adults, burrows were inspected at regular intervals every night and birds returning had their device removed after 7 or more days or deployment, were weighed then replaced in the burrow. In the case of chick-rearing adults, they were first left for 30min in the burrow to feed their chick. All 27 adults returned but 6 had lost their GPS, so in total we retrieved 21 trackers and successfully downloaded data from 19. All birds were weighed after device removal using a spring balance ($\pm 5g$). For chick-rearing adults the return mass was estimated as the mass of the adult after feeding its chick plus the overnight mass gain of the chick ($\times 0.5$ when both parents visited the nest that night).

Data processing and analysis

Only at-sea data ($>5km$ from the colony) were considered (apart from at-colony behaviour analyses), and interpolated to 1-min positions using piecewise cubic hermite polynomials in MatLab (version R2013a, The MathWorks), as in (Tremblay et al., 2006). Ground speed was calculated and a $90km/h$ threshold applied to remove erroneous positions (Guilford et al., 2008). Average flight speed was calculated on data $>7km/h$ (threshold obtained from our bimodal distribution of speed). Individual foraging trips were identified (range: 1-5 trips per individual); in total we recorded 36 trips from immatures and 29 trips from adults (6 from 6 incubating birds and 23 from 13 chick-rearing individuals).

Statistics

We used Linear Mixed Models (LMMs) to test the effect of breeding stage on foraging trip length, daily distance covered, maximum distance from the colony, and average flight speed, and Generalised Linear Mixed Models (GLMMs) to test for differences in minimum and maximum latitudes (Gamma distribution) and trip duration (Poisson distribution), with individual and year as random factors included in all models. In addition, using the bimodal distribution of trip length to choose a threshold of 3 days, we identified short and long trips and tested them separately, using

the same models, to test whether the differences observed could be accounted for entirely by trip length alone. Because all incubating trips are >3 days, and to avoid potential issues with statistical power, breeding stages were not separated in this part of the analysis. P-values were obtained by comparing our models to null models (with the random effects but without the fixed effect of interest) with a χ^2 test.

Density kernels representing the core foraging distributions were calculated using a cell size of 2km, with an optimal bandwidth of 86km estimated by a least-squares cross-validation (*sparr* package, R) (Geospatial Modelling Environment, Spatial Ecology Ltd). Distribution overlaps were estimated with the *adehabitat* package in R, and significance levels were assessed using bootstrapping (i.e. each trip was randomly allocated to the adult or immature group, a new overlap was computed and compared to the observed value; this was repeated 1000 times for each of the 25, 50 and 95% kernels).

We used Gaussian mixture models on speed and turning angle to identify different behavioural states. We used AIC to select the optimal number of states, 3, which is consistent with other mixture models run on similar datasets for the same species (Dean et al., 2013; Freeman et al., 2013). Differences in the proportion of each behaviour between breeding stages were tested with LMMs. Differences in daily patterns of the 3 states between stages were tested with Kolmogorov-Smirnov tests. Finally we tested the effect of mass on trip duration and potential differences in daily mass gain between stages with an LMM.

RESULTS

Differences in foraging trips

We compared 29 trips from 6 incubating and 13 chick-rearing adults and 36 trips from 20 immatures. The foraging trips of immatures were significantly shorter than those of incubating adults (3.7 ± 0.6 vs. 9.3 ± 1.2 days, GLMM (Poisson): $n = 42$ $Z = 3.17$, $P = 0.002$) but not of chick-rearing adults (4.9 ± 0.7 days, GLMM (Poisson): $n = 59$, $Z = 1.55$, $P = 0.121$, Figure 1a). Immatures also covered less

distance than chick-rearing adults each day (LMM: $n = 59$, $t = 2.72$, $P = 0.028$, Figure 1b), and stayed closer to the colony than all adults, even after removing one extraordinarily long incubating adult trip to the Atlantic (LMM: Imm:Egg: $n = 41$, $t = 2.49$, $P = 0.035$; Imm:Chick: $n = 59$, $t = 2.30$, $P = 0.035$, Figure 1c). Chick-rearing adults' mean flight speeds were also significantly higher than immatures' (18.2 ± 0.6 vs. 23.0 ± 0.7 km/h, LMM: $n = 59$, $t = 5.25$, $P < 0.001$, Figure 1d).

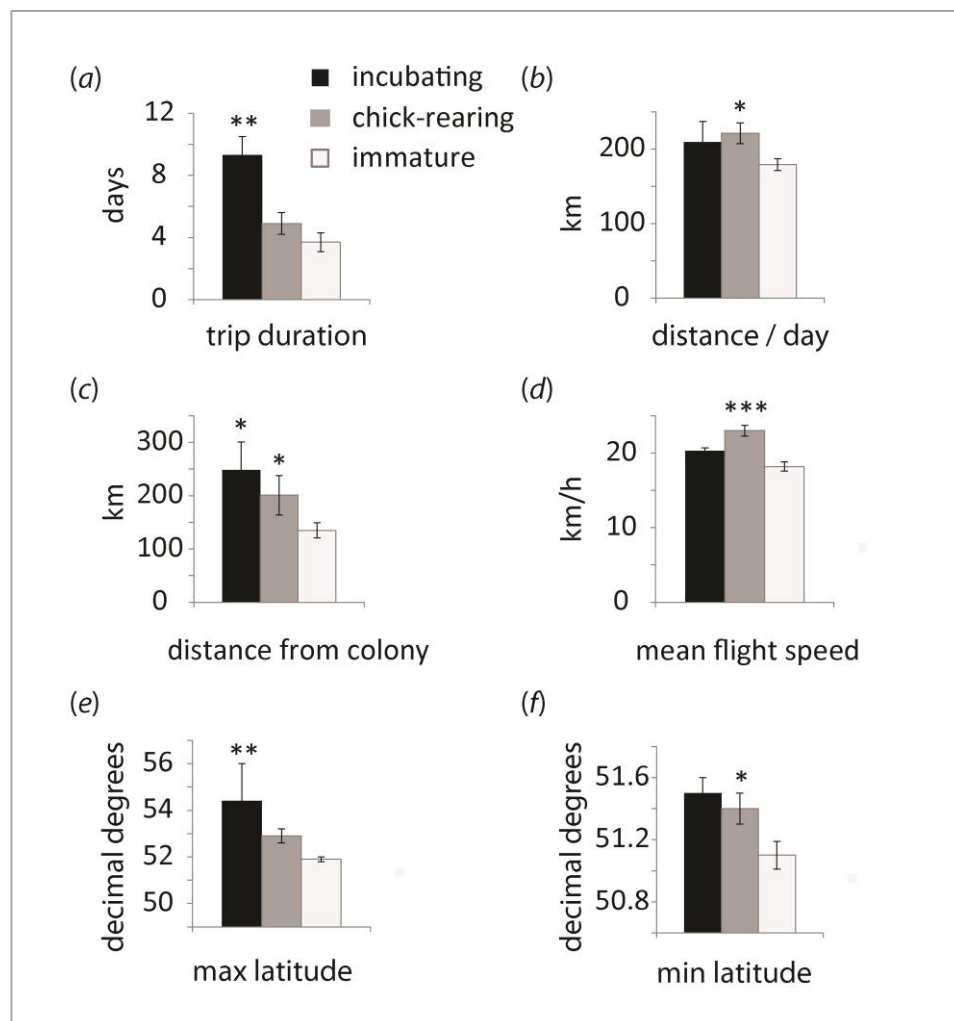


Figure 1 – Trip characteristics of immatures (white), incubating (black) and chick-rearing (grey) adults: (a) trip duration, (b) distance covered per day, (c) ,maximum distance from the colony, (d) mean flight speed, (e) maximum latitude and (f) minimum latitude (mean \pm SE). Asterisks represent significant differences between adults and immatures (*: $P < 0.05$; **: $P < 0.01$; ***: $P < 0.001$). For significance levels between incubating and chick-rearing adults see Table S1.

To investigate these differences further and test whether they could be accounted for entirely by trip length (which varied substantively between immatures: range 1-15 days), we analysed short and long trips separately. The distribution of trip durations was bimodal, which allowed us to identify a threshold of 3 days to classify trips as long (> 3 days, $n_{\text{immature}} = 15$, $n_{\text{adult}}=19$) or short (≤ 3 days, $n_{\text{immature}} = 21$, $n_{\text{adult}}=10$). Adults covered more distance each day but the difference was only significant on short trips (LMMs: short trips: $n = 31$, $\chi^2 = 9.04$, $P = 0.003$; long trips: $n = 34$, $\chi^2 = 3.75$, $P = 0.052$). They still travelled further from the colony but only on long trips, even without the long adult trip to the Atlantic (LMMs: short trips: $n = 31$, $\chi^2 = 0.01$, $P = 0.919$; long trips: $n = 33$, $\chi^2 = 6.36$, $P = 0.012$). Adults' mean flight speed remained higher than immatures' in both short and long trips (LMMs: short trips: $n = 31$, $\chi^2 = 15.94$, $P < 0.001$; long trips: $n = 34$, $\chi^2 = 5.55$, $P = 0.018$). Details of all means \pm SE and statistics are presented in Table S1.

Spatial segregation

We found significant differences between the destinations of adult and immature birds. On average, adults went to significantly higher latitudes than immatures (GLMM (Gamma): $n = 65$, parameter estimate : $5.4 \text{ E-}4 \pm 2.6\text{E-}4$, $t = 107.4$, $P = 0.029$, Figure 1e); while immatures went significantly further south (GLMM (Gamma): $n = 65$, parameter estimate : $2.0 \text{ E-}4 \pm 0.8\text{E-}4$, $t = 200.1$, $P = 0.013$, Figure 1f). This held when we looked at short and long trips separately (Table S1). There were differences between the occupancy contours of adults and immatures, at the 95%, 50% and 25% density levels. The overlap of the core distributions of adults and immatures, which was below 20% at the 50% occupancy level and below 5% at the 25% occupancy level, was significantly lower than expected by chance at the 25% and 50% level (25%: 4% overlap, $P = 0.020$; 50%: 19% overlap, $P = 0.045$, 95%: 83%, $P = 0.377$, P-values obtained from bootstrapping with a 1000 iterations, Figure 2). These differences were not due to different trip durations between groups, as the overlap between adults and immatures remained small when looking at short and long trips separately (Figure 2c). Overlap of core distributions occurred near the colony, near the southern Irish coast and in the

214 middle of the Celtic Sea. The most striking segregation was in the Irish Sea, which was visited by a
215 single immature but over 50% of adults. This was not due to the Irish Sea trips taking too long for
216 immatures: all adult trips in the Irish Sea lasted 6-12 days and only one of seven immature trips in
217 this range of duration was to the Irish Sea (vs 10 of 18 for adults). Rather than the Irish Sea, the
218 south Celtic Sea and around the Cornish peninsula were preferred by immatures; over 40% ventured
219 south of the Bristol Channel and even south of the UK into the Channel, while only 10% of the adults
220 went to such low latitudes (and none to the Channel). Both groups foraged in the Celtic Sea, but
221 more adults favoured the Irish south coast while more immatures foraged along the coast of North
222 Wales.

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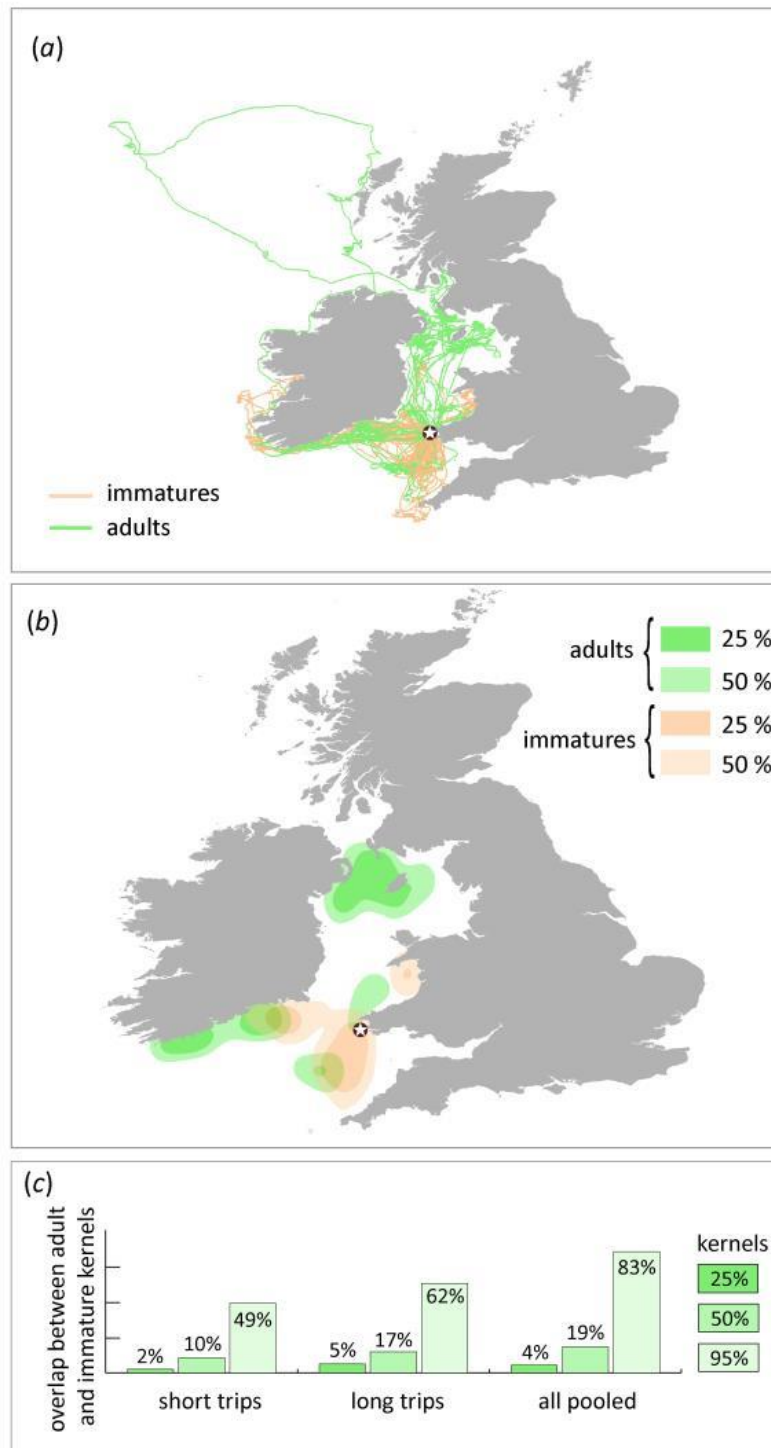


Figure 2. (a) Raw tracks from the 20 immature (orange) and 19 adult (green) shearwaters in 2013 and 2014. (b) 50% and 25% occupancy kernels of immatures and adults calculated on the whole dataset. The colony is indicated with a star. (c) Overlap between 25%, 50% and 95% occupancy kernels of adults and immatures, with all trips pooled ($n = 65$) or separated by trip duration (short: $n = 31$; long: $n = 34$).

At-sea behaviour

The optimum number of behavioural states identified with our Gaussian mixture model was 3. The three states are taken to identify approximately foraging (low speed, high turning angle), sustained flight (high speed, low turning angle) and resting (low speed, low turning angle) (Table 1, Figure 2).

	Ground Speed (km/h)	Turning angle (°)	proportion in incubating adults (%)	proportion in chick-rearing adults (%)	proportion in immatures (%)
Class 1: “foraging”	5.85 ± 0.10	129.56 ± 0.52	17.5 ± 0.1	14.0 ± 0.8	14.1 ± 0.5
Class 2: “sustained flight”	34.19 ± 0.20	19.32 ± 0.47	13.8 ± 3.1	16.0 ± 1.6	11.1 ± 1.0
Class 3: “resting”	4.01 ± 0.04	21.35 ± 0.21	68.6 ± 3.2	69.9 ± 1.4	74.7 ± 1.0

Table 1. Metrics of the 3 classes of behaviour as identified by a Gaussian mixture model.

Birds spent most of their time “resting” on the water, with “foraging” the second and “sustained flight” the least common behavioural class at sea. All adults and immatures spent similar proportions of time flying (LMM: Imm_Egg: parameter estimate 0.03 ± 0.03 , $t = 0.92$, $P = 0.60$; Imm_Chick: parameter estimate 0.04 ± 0.02 , $t = 2.4$, $P = 0.51$; Egg_Chick: parameter estimate -0.02 ± 0.03 , $t = -0.63$, $P = 0.70$). However, immatures spent less time foraging and more time resting than incubating adults (LMMs: foraging: Imm_Egg: parameter estimate 0.03 ± 0.01 , $t = 2.34$, $P = 0.023$; Imm_Chick: parameter estimate -0.005 ± 0.01 , $t = -0.06$, $P = 0.33$; Egg_Chick: parameter estimate -0.03 ± 0.02 , $t = -2.33$, $P = 0.07$; resting: Imm_Egg: parameter estimate -0.06 ± 0.02 , $t = -2.24$, $P = 0.044$; Imm_Chick: parameter estimate -0.05 ± 0.02 , $t = -2.56$, $P = 0.134$; Egg_Chick: parameter estimate 0.006 ± 0.03 , $t = 0.23$, $P = 0.65$).

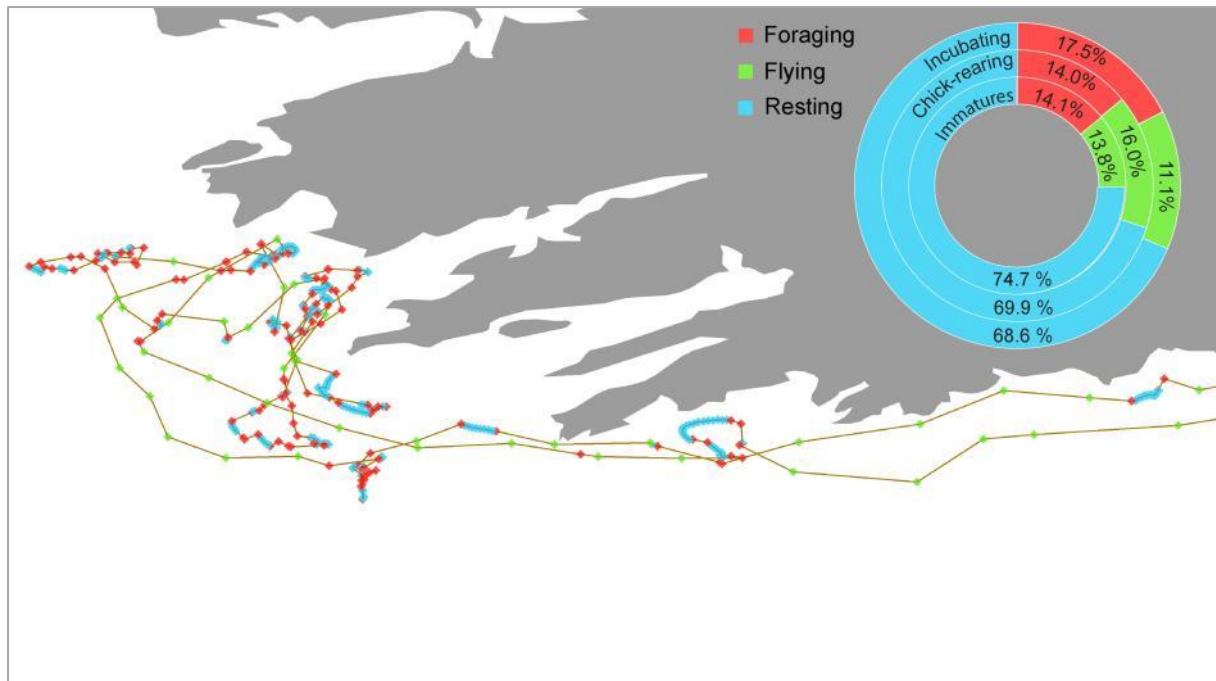


Figure 3. Example of behavioural classification of part of a foraging trip, and proportions of time spent foraging (red), flying (green) and resting (blue) for immatures, incubating and chick-rearing adults across whole dataset.

Despite adults and immatures travelling to largely separate locations, the patterns of daily activity were similar between stages (KS tests, $N_{imm} = 16$, $N_{egg} = 6$, $N_{chick} = 13$: foraging: $D_{imm:egg} = 0.17$, $P = 0.89$, $D_{imm:chick} = 0.20$, $P = 0.67$, $D_{egg:chick} = 0.25$, $P = 0.44$; flying: $D_{imm:egg} = 0.25$, $P = 0.44$, $D_{imm:chick} = 0.33$, $P = 0.14$, $D_{egg:chick} = 0.25$, $P = 0.44$; resting: $D_{imm:egg} = 0.25$, $P = 0.44$, $D_{imm:chick} = 0.13$, $P = 0.99$, $D_{egg:chick} = 0.21$, $P = 0.67$) (Figure 4), and were also similar to timings previously found in this species (Dean et al., 2013). Foraging occurred across daylight hours with a slight increase towards the end of the afternoon. Resting occurred most at night, but also occupied a significant part of the day, especially the middle. Flying occurred predominantly by day, with distinct peaks around sunrise and before sunset, when birds left or arrived near the colony.

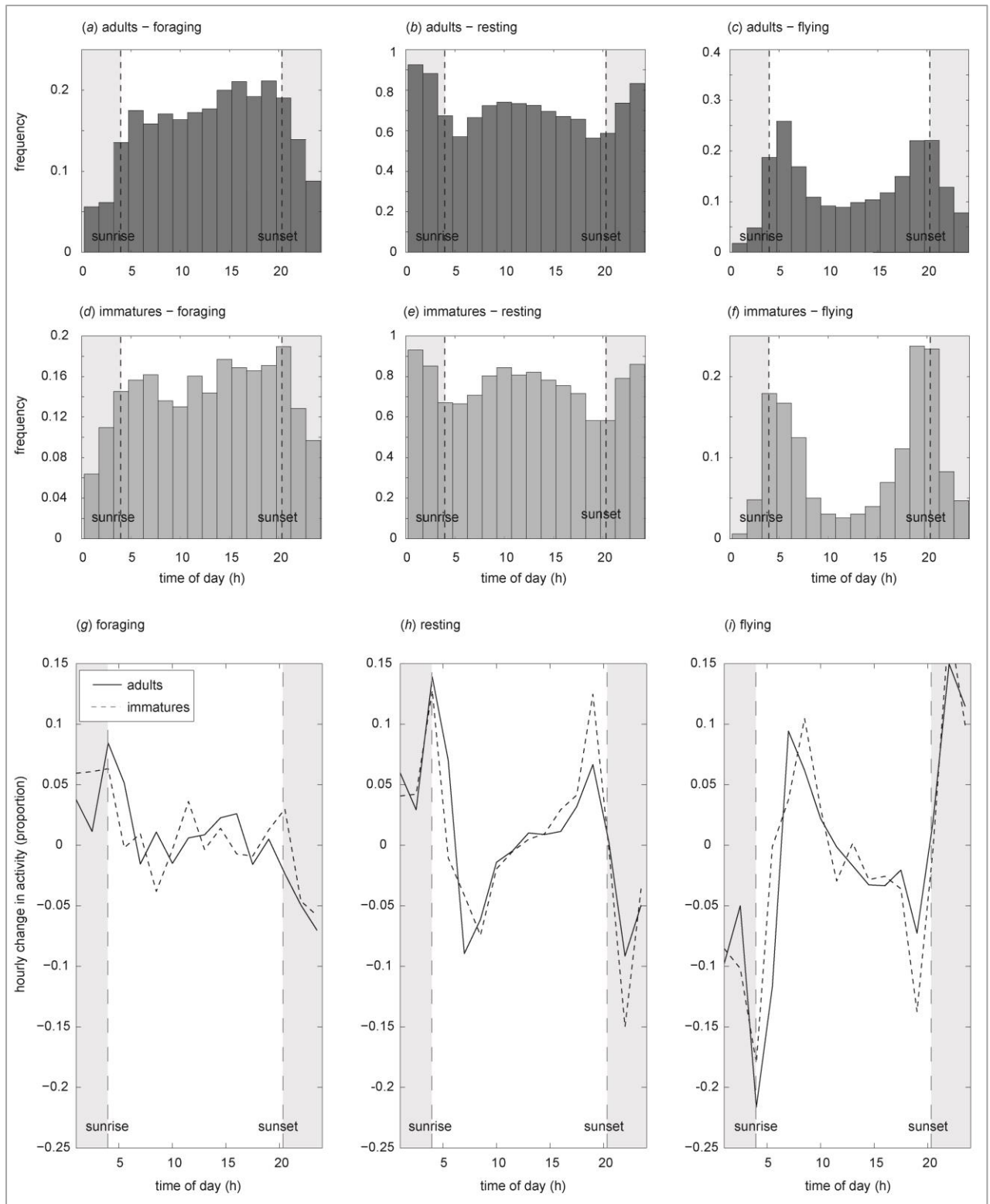


Figure 4. Stacked histograms of (a) foraging, (b) resting and (c) flying behaviours against time of day for adults (dark grey) and immatures (light grey), and their hourly variation (d), (e), (f) for adults (continuous lines) and immatures (dashed lines). The y-axis represents a change in proportion, e.g. if the proportion of adults flying is

10% between 4-5pm and 25% between 5-6pm, the value for 5pm will be 0.15. On all 6 panels night time is represented with a light grey background, and sunrise and sunset with grey dashed vertical lines.

Daily mass gain

Immature birds were significantly lighter than adults prior to tracking ($364 \pm 5\text{g}$ vs. $405 \pm 5\text{g}$; $N_{imm} = 20$, $N_{ad}=19$; T-test: $t_{36,9}=5.59$, $P < 0.001$). Lighter immatures tended to go on shorter foraging trips (LMM, $N = 20$, parameter estimate: $0.01 \pm 4.1\text{E-}3$, $Z=3.17$, $P = 0.002$), but this was not the case in adults, even when controlling for breeding stage (LMM, $N = 19$, parameter estimate: 0.002 ± 0.004 , $Z=-0.56$, $P = 0.58$). In addition, immatures gained significantly less mass per day ($-0.59 \pm 0.7 \text{ g.day}^{-1}$ on average) than incubating birds ($5.6 \pm 1.8 \text{ g.day}^{-1}$ on average; LMM: parameter estimate: 6.22 ± 1.69 , $t = 3.7$, $P < 0.001$) and chick-rearing-birds ($2.0 \pm 0.9 \text{ g.day}^{-1}$ on average; LMM: parameter estimate: 2.59 ± 1.29 , $t = 2.0$, $P=0.05$), while adults also differed significantly between stages (LMM: parameter estimate: 3.63 ± 1.79 , $t = 2.0$, $P=0.05$). To check whether the differences in efficiency were simply an effect of size, we tested whether bird mass had an effect on efficiency (mass gain per unit of time spent foraging) in adults and immatures: we did not find any significant differences in adults and a nearly significant trend in immatures (LMMs: immatures: $N = 20$, parameter estimate: -0.01 ± 0.005 , $\Delta\text{logLik} = 1.88$, $\Delta\text{AIC} = -1.75$, $\chi^2_1 = 3.76$, $P=0.053$, adults: $N = 19$, parameter estimate: -0.11 ± 0.8 , $\Delta\text{logLik} = 1.11$, $\Delta\text{AIC} = -0.21$, $\chi^2_1 = 2.21$, $P=0.137$). The trend was negative, i.e. heavier immatures tended to be less efficient than lighter immatures.

DISCUSSION

By comparing simultaneously precision tracked foraging trips of different life-stages we were able to investigate the foraging distributions of immatures and breeding adults under identical environmental circumstances. At the same time, we used an etho-informatics analysis, and a proxy for foraging success (mass gain), to estimate individual foraging efficiencies. We found that immatures were substantially spatially segregated from adults in their foraging destinations, and that

this was not an effect of constraints on trip duration or flight distance: on average immatures foraged closer to the colony than adults, their trips were of similar duration than the trips of chick-rearing adults (but shorter than incubating trips). In addition, they covered similar distances per day, and at similar flight speed, to incubating birds (but shorter distances and at lower flight speed than chick-rearing adults). Although there are small differences in measured speeds and trip durations between immatures and chick-rearing (though not incubating) adults, which may indicate that immatures are less efficient in sustained flight, these differences are not sufficient to deny immatures access to the core areas exploited by adults in our study. Critically, we found that for the same amount of time spent engaged in foraging-related behaviour, immatures gained less mass, suggesting that they are less efficient at foraging than adults. There are several potential causes of this effect. One possibility is that immatures are inferior competitors because they are lighter than adults (~10% lighter in our dataset), and are competitively excluded from the best foraging areas. However we found no evidence that heavier birds were better at foraging – we found no effect of mass on foraging efficiency in adults, and only a nearly-significant trend in immatures, but negative, indicating that heavier immatures do not forage more effectively. Furthermore, we found that whilst lighter immatures did go on shorter trips, this was not the case in adults, whether they were incubating an egg or rearing a chick. Thus, the differences we observe between adults and immatures cannot be readily explained by size differences alone.

Alternatively (or in addition), immatures may be less effective foragers because they lack individually acquired experience which may enable adults to recall the locations of the best foraging areas under different conditions, recognise the signals indicative of prey presence, or hunt prey more effectively (e.g. by diving at different depths; Le Vaillant et al., 2012), in an environment where prey is patchy, often ephemeral, and predictable only on a complex spatio-temporal scale. In our dataset, the clearest segregation occurred in the Irish Sea: over 50% of adults visited the Irish sea front (a known seabird hotspot for several species including Manx shearwaters; Begg & Reid, 1997; Pollock, Reid, Webb, & Tasker, 1997), but no immature did, even though it was well within their range (in duration

and distance); it seems unlikely that this absence can simply be explained by their inability to find this area, where large flocks of Manx shearwaters can be seen flying to and from during the breeding season (Durazo, Harrison, & Hill, 1998). This suggests that immatures were competitively excluded from this area. The only immature going to the Irish Sea (which did not reach the front) was one of the heaviest (3rd/20) and within the range of adult mass; furthermore unlike the other immatures we tracked it shared the same burrow each night with the same bird (with a small brood patch), and remained in a burrow for 24h on two occasions during the tracking period. This suggests that this bird was most likely a pre-breeder with a newly established burrow or a breeder who failed early enough in the season for its brood patch to disappear. There may be a threshold (triggered by mass, age or experience) above which it becomes worth facing intraspecific competition in the Irish Sea. This may also be the same threshold which triggers the start of breeding, as is also observed in albatrosses (Weimerskirch, 1992).

Poorer foraging ability in immatures has often been invoked as the main reason for the higher immature mortality observed in many species (Ashmole, 1963; Lack, 1954). Immatures' improvement of foraging with experience has been demonstrated in several taxa (Lefebvre, 1995; Mazur & Seher, 2008) including seabirds (Daunt et al., 2007; Yoda, Kohno, & Naito, 2004), and may continue after reaching adulthood (Haug, Paiva, Werner, & Ramos, 2015). Furthermore, Manx shearwaters are known to increase in mass until at least age 6 (Brooke, 1978). Tracking data of immature wandering albatrosses visiting their colony during the breeding season revealed that immatures, like our shearwaters, took shorter trips than breeding adults and covered shorter distances; the authors suggested that immatures may stay nearer the colony (where they are likely to experience higher competition for resources) to learn how to deal with the competition constraints of central-place foraging near the colony, which they will have to deal with once they start breeding (Riotte-Lambert & Weimerskirch, 2013; Weimerskirch et al., 2013). On the other hand, a study in gannets found that immature gannets covered longer distances and went on longer trips than chick-rearing adults between regular visits to the colony, interestingly also visiting other

colonies during their trips (Votier et al., 2011). Here, the authors argued the longer trips of immature gannets were a way to avoid high intra-specific competition near the colony. The limitation of these studies is that the tracking of immatures and adults was not simultaneous but occurred in different years, and so the differences may be masked or enhanced by different environmental conditions.

CONCLUSION

Our study reveals for the first time the simultaneous foraging movements of adult and immature seabirds during the breeding season, hereby addressing the issue of between-year differences in environmental conditions potentially confounding the findings of previous studies. In addition, by measuring the foraging success of the birds, we can estimate and compare foraging efficiency between immatures and breeders. Our findings highlight substantial spatial segregation between adults and immatures during central place foraging around the colony, and lower foraging efficiency in immatures, which is not driven by size differences and therefore most likely due to inexperience. This is driving the spatial segregation we observe by excluding the inferior competitors (immatures) from the better foraging areas visited by adults. Our findings provide the strongest evidence to date that within-species spatial segregation in long-lived animals can be driven by differences in foraging experience, which may in turn lead to intra-specific competition.

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