Article

Immature gannets follow adults in commuting flocks providing a potential mechanism for social learning

Ewan D. Wakefield, Robert W. Furness, Jude V. Lane, Jana W. E. Jeglinski and Simon J. Pinder

E. D. Wakefield (https://orcid.org/0000-0002-2586-1232) ✉ (ewan.wakefield@glasgow.ac.uk), R. W. Furness and J. W. E. Jeglinski, Univ. of Glasgow, Inst. of Biodiversity, Animal Health and Comparative Medicine, Graham Kerr Building, Glasgow, UK. – J. V. Lane, School of Biology, Faculty of Biological Sciences, Univ. of Leeds, Leeds, UK. – S. J. Pinder, MARINElife, Bridport, UK.

Group travel is a familiar phenomenon among birds but the causes of this mode of movement are often unclear. For example, flocking flight may reduce flight costs, enhance predator avoidance or increase foraging efficiency. In addition, naive individuals may also follow older, more experienced conspecifics as a learning strategy. However, younger birds may be slower than adults so biomechanical and social effects on flock structure may be difficult to separate. Gannets are wide-ranging (100s–1000s km) colonial seabirds that often travel in V or echelon-shaped flocks. Tracking suggests that breeding gannets use memory to return repeatedly to prey patches 10s–100s km wide but it is unclear how these are initially discovered. Public information gained at the colony or by following conspecifics has been hypothesised to play a role, especially during early life. Here, we address two hypotheses: 1) flocking reduces flight costs and 2) young gannets follow older ones in order to locate prey. To do so, we recorded flocks of northern gannets commuting to and from a large colony and passing locations offshore and used a biomechanical model to test for age differences in flight speeds. Consistent with the aerodynamic hypothesis, returning flocks were significantly larger than departing flocks, while, consistent with the information gathering hypothesis, immatures travelled in flocks more frequently than adults and these flocks were more likely to be led by adults than expected by chance. Immatures did not systematically occupy the last position in flocks and had similar theoretical airspeeds to adults, making it unlikely that they follow, rather than lead, for biomechanical reasons. We therefore conclude that while gannets are likely to travel in flocks in part to reduce flight costs, the positions of immatures in those flocks may result in a flow of information from adults to immatures, potentially leading to social learning.

Keywords: central-place foraging, colonial breeding, cultural transmission, information centre hypothesis, social learning, spatial segregation

Introduction

Many birds travel in groups, but this subjects individuals to greater competition than lone travel. Group travel must therefore afford compensatory advantages (Alexander 1974, Herbert-Read 2016). For example, by travelling in flocks, geese, swans and

1

cranes reduce aerodynamic drag and therefore save energy (Lissaman and Shollenberger 1970, Weimerskirch et al. 2001, Portugal et al. 2014). In addition, group travel can improve foraging efficiency, navigational accuracy and predator avoidance (Brown and Brown 2001). It is also becoming apparent that it may have additional social functions (Herbert-Read et al. 2013). Specifically, flocks can form due to poorly informed individuals following better informed conspecifics in order to gain information (Dall et al. 2005). For example, naïve common ravens *Corvus corax* follow conspecifics that have recently discovered the locations of carrion (Marzluff et al. 1996) and immature whooping cranes *Grus americana* learn migratory routes by following older conspecifics (Mueller et al. 2013). Group travel can therefore facilitate social learning (Hoppitt and Laland 2013). In practice, there may be multiple reasons why animals travel in groups in a particular context. Understanding the phenomenon may therefore provide insights into the way that physical, ecological and social processes interact (Alexander 1974, Herbert-Read 2016). Here we consider the potential functions of group travel among gannets (*Morus* spp.) – large, wide-ranging pelagic seabirds, which frequently travel in flocks (Nelson 2006). In particular, we ask whether the structure of gannet flocks provides any evidence to support two not necessarily mutually exclusive hypotheses: firstly, that immature gannets travel in groups in order to reduce flight costs and secondly that they do so to locate prey.

At sea, gannets gravitate to feeding conspecifics within their visual range (Nelson 2001, Tremblay et al. 2014). This process, known variously as local enhancement (Galef and Giraldeau 2001) or network foraging (Wittenburger and Hunt 1985), explains why gannets frequently form flocks on foraging grounds. However it does not explain why they also commute between their colonies and foraging areas in flocks, which they do frequently (Nelson 2001, Jones et al. 2018). It is unlikely that group commuting is primarily a predator defence strategy: gannets are rarely predated by other birds at sea (Barrett 2008) and although northern gannets *Morus bassanus* are sometimes kleptoparasited by great skuas *Stercorarius skua* this threat is largely confined to the northern part of their range during the breeding season, yet gannets travel in flocks throughout their range. We do not therefore consider predation as a fundamental driver of flocking here.

The hypothesis that gannets form flocks for reasons of aerodynamic efficiency has not been tested directly but is suggested by the observation that flocks of commuting gannets are often 'V' or echelon shaped (Nelson 2001). In other large birds, these formations emerge only when individual flock members position themselves in the maximum backwash of preceding individuals (Lissaman and Shollenberger 1970, Weimerskirch et al. 2001, Portugal et al. 2014). If gannets do indeed travel in flocks to save energy, one might expect them to do so more frequently and in larger groups during return flights to the colony (prediction 1, Table 1) simply because return flight paths converge on the colony. In addition, theory predicts that energetic savings due to flock formation are greater in upwind than downwind flight (Lissaman and Shollenberger 1970). If group travel has an aerodynamic cause, commuting gannets might therefore be expected to travel in flocks more frequently when encountering headwinds (prediction 2).

Evidence suggesting that gannets travel in groups to locate prey is more circumstantial, and therefore requires more detailed explanation: gannets foraging from colonies only tens of km apart overlap little, despite the fact that they often forage hundreds of km from their colonies (Grémillet et al. 2004, Wakefield et al. 2013). Although this is ultimately thought to be due to density-dependent competition, it has been hypothesised to be an emergent, group-level behaviour, mediated by public information transfer among colony members (Grémillet et al. 2004, Wakefield et al. 2013). In short, simulations show that if and only if information flows among conspecifics, colony members tend to avoid areas where scramble competition from members of adjacent colonies is high. In time, information is passed from generation to generation, allowing colony specific foraging areas to perpetuate and diverge (Wakefield et al. 2013). The mechanisms through which public information might be transmitted were originally posited as part of the information centre hypothesis (ICH; Ward and Zahavi 1973). This hypothesis proposes that colonial birds, such as gannets, gain public information either by observing the return directions of successful conspecifics to the colony or by following those

Table 1. Predictions following from hypothesised reasons that northern gannets travel in flocks and that these flocks are structured by age.

Hypotheses and predictions	Supported	Notes
Group travel reduces aerodynamic cost		
1. Inward commuters travel in flocks more than outward commuters	Yes	
2. Travel in flocks more frequent in headwinds than in tailwinds	Yes/No	Ambiguous (see text)
Group travel allows public information transfer		
3. Outward commuters travel in flocks more than inward commuters	No	
4. Immatures travel in flocks more frequently than adults	Yes	
5. Adults lead mixed-age flocks	Yes	But unaffected by direction
6. Oldest bird leads immature flocks	Yes	
Flock leadership dictated by speed or motivation		
7. Immatures slower than adults	(No)	Inferred from morphology
8. Within mixed-age flocks, youngest bird occupies the last position	No	

individuals from the colony to prey patches. Evidence consistent with the first process includes the observation that Cape gannets *M. capensis*, leaving the colony to forage, head in the opposite direction to returning conspecifics, a behaviour associated with shorter times to first dives (Thiebault et al. 2014a). In addition, Australasian gannets *M. serrator* have been shown to join rafts of conspecifics near the colony prior to departure (Machovsky-Capuska et al. 2013). Among Guanay cormorants *Phalacrocorax bougainvillii*, a similar behavior cues birds on the direction of ephemeral prey patches (Weimerskirch et al. 2010). If gannets do indeed follow one another purely to gain information on the location of prey, then birds leaving the colony might be expected to travel in flocks more frequently than those returning from it (prediction 3). However, to date, no study has shown that poorly informed gannets selectively follow better informed individuals. This is in part because it is difficult for human observers to distinguish informed from uninformed individuals. Moreover, adult gannets may resort to public information use infrequently, relying on memory to locate prey patches much of the time (Hamer et al. 2000, Patrick et al. 2014, Wakefield et al. 2015).

In general, immature animals are expected to be less well informed than adults and therefore more likely to seek public information (Hoppitt and Laland 2013). Immatures gannets are easily distinguished from adults by their darker plumage (Nelson 2001). Behaviours consistent with information transfer could therefore not only be more frequent within mixed-age groups of gannets but also more readily observable. Having fledged, the majority of northern gannets migrate to waters off west Africa. They begin breeding around age six years but attend breeding colonies from their second or third summers (Nelson 2001). During the latter period, they may visit multiple colonies but the majority of their movements comprise repeated foraging trips to and from one colony (Votier et al. 2011, 2017, Grecian et al. 2018). In contrast to adults, immatures visit different foraging locations on each successive foraging trip (Votier et al. 2017). Votier et al. hypothesise that this is because immatures are relatively poorly informed about the distribution of prey, and therefore more exploratory in their behaviour (rather than because they are displaced by adults from the most favourable foraging patches). Assuming that immatures are less well informed, the ICH predicts that they will frequently follow adults from the colony in order to locate prey (Ward and Zahavi 1973). Conversely, adults should avoid following immatures. If correct, immatures should travel in flocks more frequently than adults (prediction 4) and mixed-age flocks should be led by adults more frequently than expected by chance (prediction 5). Similarly, if gannets learn the locations of prey patches gradually as they mature, flocks of immatures of different ages should be led by the oldest bird (prediction 6). However, if gannets travel in flocks purely for reasons of aerodynamic efficiency, adults could travel at the front of such flocks for several other reasons: firstly, if adults are larger, they would fly faster than immatures, because airspeed scales with mass and wing size (Alerstam et al. 2007, Pennycuick

2008). Similarly, differences in tissue mass or physiology could result in differences in flight performance among age groups (Pennycuick 1989). Thirdly, immatures could be less motivated to commute rapidly than adults, because the latter are more time-constrained due to their reproductive duties (Conradt et al. 2009). Finally, immatures could simply be less proficient fliers than adults (Flack et al. 2018). The first possibility (prediction 7) can be examined using morphological data. The other effects are less easy to quantify. However, if immatures were slower than adults for any of the above reasons, we would expect younger birds to occur disproportionately in the last position in mixed-aged flocks (prediction 8).

To test the predictions outlined above, we observed gannets commuting to and from the Bass Rock (56°6′N, 2°36′W), the world's largest northern gannet colony (~75 300 breeding pairs (Murray et al. 2014)), and at various locations offshore. We then modelled how frequently gannets travel in flocks and the sizes of those flocks as functions of age, wind conditions and flight direction (to/from the colony). We considered the possibility that immatures are slower than adults indirectly, by testing whether immatures occupy the last position in mixed-age flocks and whether morphology differs sufficiently between adults and immatures to result in differing theoretical flight speeds.

Material and methods

Data collection

During June and August 2014 and 2018, gannets were observed from land-based vantage points (VPs) in the vicinity of the Bass Rock (BR). By referring to the movements of gannets tracked during preceding breeding seasons (Hamer et al. 2000, Wakefield et al. 2013, 2015), we selected three VPs that afforded clear views of gannets commuting between BR and foraging areas to the north-northeast and southeast. VPs were located on the Isle of May (IM), 13 km from BR; Fife Ness (FN), 23 km from BR; and St Abbs Head (SA), 36 km from BR. SA is a headland with 50–100 m high cliffs, whereas FN and IM are low (10 m) headlands, the latter located at the end of a 2 km long island.

All land-based data was collected by the first author, who has extensive seabird survey experience. Gannets passing VPs were observed using 10 × 42 binoculars and a 20 × 60 telescope. Measurements using digital photographs indicated that the maximum apparent separation distance within clearly defined groups of commuting gannets ranged from 0.1 to 9.4 bird-lengths (median 2.5, n = 50 groups). We therefore nominally defined flocks as groups of at least two birds flying in the same direction, with a maximum apparent separation between individuals of ten bird-lengths. We refer to gannet age in calendar years (cy), commencing at 1 at birth and advancing every 1st January. Plumage indicates the approximate age of immature gannets, although some individuals attain adult-type plumage by cy 4 (Nelson 2001). Hereafter, we use 'mixed-age' to refer to flocks containing adults and

immatures and 'mixed-immature' to refer to flocks containing immatures of different ages (immatures were assumed to be those in 2nd to 5th cy type plumage). Adult flocks could also contain individuals of different ages, but the age of adult gannets cannot be determined from external characteristics. Only birds passing within 500 m of VPs were recorded (trials using digital photography and a rangefinder (Heinemann 1981), showed that plumage types could be discriminated reliably up to this distance). Feeding gannets tend to aggregate. Although tracking data show that adult gannets rarely feed in the vicinity of the VPs (Wakefield et al. 2015), if any feeding was detected within 2 km of VPs observations were suspended until 10 min after this activity had ceased to avoid this confounding aggregation for aerodynamic or information gathering reasons.

We recorded gannets engaged in direct flight (continuous flight in one direction ≥ 20 s) as they passed a notional line perpendicular to the birds' main flight path. We assumed that all birds observed in direct flight towards or away from BR were commuting to and from the colony, acknowledging that a small proportion may have had other destinations/origins. Due to the large number of birds passing VPs, it was not practicable to accurately record all data required simultaneously. Rather, recording was carried out in sequential bouts, repeated in the following order: during bout #1 (10 min), group size for all gannets travelling alone or in flocks towards or away from BR was recorded. During bout #2 (10 min), both this information, plus the proportion of immatures in each group was recorded. Finally, during bout #3 (30–60 min), the age and positions of immatures within all mixed-age and mixed-immature flocks passing to or from the colony were recorded – i.e. we recorded the putative age and rank order of each bird within each flock, counting the latter from the front to the back of the flock. Multiple observation bouts were carried out throughout daylight hours at each VP and data from more than one bout type were merged where appropriate for some analyses. Every 20 min, the wind speed and direction measured using a handheld anemometer (Skywatch Eole, JDC Electronics, Switzerland) was also recorded. Subsequently, we calculated the wind speed at a reference height of 12 m (the median flight height of commuting gannets (Cleasby et al. 2015)) using a logarithmic model (Pennycuick 1982). We then calculated the vector component of wind speed contra to the heading of each flock (hereafter, headwind).

In order to test whether flocks are age structured remote from colonies or other land, we also recorded the age structure of gannet flocks travelling over the open sea. These data were collected opportunistically during boat-based surveys in May–September, 2013 and 2015 (Supplementary material Appendix 1 Table A1) in various areas at an average of 14.3 km (range 0.5–20 km) from the UK coast and 61 km from the nearest gannet colony (range 14.5–116.3 km). During these surveys, seabirds were recorded using standard European Seabirds at Sea (ESAS) methods (Camphuysen et al. 2004). In brief, this involved recording birds while the vessel was underway at speeds of 7–10 knots, following a survey pattern designed for seabird abundance and distribution estimation

for purposes other than this study. All seabirds within or passing through a 300 m wide strip transect running parallel to the vessel's track were detected by an observer using the naked eye or 10 × 42 binoculars. Data, including species, age and group size, were recorded by a second surveyor, who also recorded Beaufort wind force and direction at the start and end of transects and every 30 min. In addition, for the purposes of the current study, the ages and positions of all members of mixed-age gannet flocks detected in direct flight were recorded (flocks and direct fight were defined as above). Data were collected by five ESAS-qualified surveyors, all of whom had at least 100 h of seabird survey experience.

To test for morphologically mediated differences in flight speed, we measured immature and adult gannets on BR. We caught birds during July and August 2016 using a hook or metal noose attached to a 5 m pole and measured their mass (± 20 g) and wing semi-span (i.e. spine to the wing tip, ± 1 mm) and photographed one wing, laid flat and fully extended on a board marked with a 5 cm grid. We then geo-referenced wing images in QGIS Desktop 2.14.3, corrected for lens distortion, digitized the wing outlines (from the root chord to the wing tip) and calculated the partial wing area. We then calculated the total wing area as twice the partial area, plus the intervening body section (Pennycuick 2008).

Analysis

We carried out all analyses in R (R Development Core Team). Hereafter, we refer the first bird in a flock as the leader and all other birds in the flock as followers. Unless otherwise stated, we use these terms to denote position, not social rank or function. We modelled the effects of wind, travel direction and age on flock formation, size and leadership (predictions 1–6), using mixed-effects generalized linear models (GLMMs), fitted using the lme4 package (Bates et al. 2015). We specified random intercepts for each VP, and simplified models by backwards selection from the maximal model (i.e. that containing all candidate covariates and their interactions) using likelihood ratio tests (LRTs) (Bolker et al. 2009). We specified either binomial or negative binomial errors as appropriate to the data (see Results). We checked for overdispersion and that the data conformed to model assumptions using Q–Q plots and plots of residuals versus fitted values generated using the DHARMa package (Hartig 2018).

To determine whether adults led mixed-age flocks more frequently than expected by chance (prediction 5), we used a one-sided permutation test (Edgington and Onghena 2007), coded in R as follows: we defined the test statistic, t, as the proportion of mixed-age flocks led by an adult, which we first calculated for the observed data (t_{obs}). We then randomly shuffled the age of individuals within flocks and recalculated the test statistic (t_{perm}). We repeated this step, shuffling age in $m = 10\,000$ unique permutations. The distribution of t_{perm} approximates distribution of t under the null hypothesis that age is exchangeable within flocks. We calculated the probability p, that t_{obs} occurred under this hypothesis as $p = (b_t + 1)/(m + 1)$, where b_t is number of t_{perm} greater than t_{obs}. This is

effectively the probability that the observed proportion of adult-led flocks was greater than that expected by chance. We used the same procedure to test prediction 6, that the oldest birds occupied the front position in flocks comprising only immatures (mixed-immature flocks). We also used a similar procedure to test whether immature birds systematically occupied the last position among mixed-age followers within flocks (prediction 8). In this case, t_{obs} was the proportion of such flocks in which an immature occupied the last position in the flock. To estimate the distribution of this statistic under the null hypothesis that age is exchangeable among followers, we shuffled the age of following birds randomly 10 000 times, calculating t_{perm} each time. For this test to operate, it was necessarily limited to flocks containing ≥ 2 followers, including at least one adult and one immature. For each permutation test, we report p, t_{obs}, median t_{perm} and its 95% confidence interval (CI).

To test for morphologically mediated differences between the flight speeds of adults and immatures (prediction 7), we used Pennycuick's (2008) biomechanical model, implemented in Flight 1.24 for Windows, to predict the theoretical flight speeds of the gannets that we measured on the Bass Rock. Using the morphometrics, we predicted their minimum power speeds V_{mp} and maximum range speeds V_{mr} in flapping flight and minimum sink speeds V_{ms} and best glide speeds V_{bg} in soaring flight.

Data deposition

Data available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3rg5307> (Wakefield et al. 2019).

Results

Gannets observed from land

Land-based observations were made between 05:24 and 20:40 GMT from FN, IM and SA during 5, 2 and 3 d, respectively (Supplementary material Appendix 1 Table A1). Wind speed at Leuchars, the nearest coastal weather station to BR averaged 4.7 m s^{-1} (range 1.2–7.6 m s^{-1}) during the data collection period, which is similar to the June–August, long-term, average of 4.2 m s^{-1} (UK Meteorological Office 2018). Data collection lasted a total of 400, 420 and 240 min at FN, IM and SA respectively, during which time a total of 3657 individuals and 709 flocks were recorded. During the three different data collection activities, we recorded 1) group size for 1237 individuals and 204 flocks; 2) group size, plus the number of immatures in those groups for 1012 individuals and 179 flocks and 3) the age structure of 255 mixed-age and 71 mixed-immature flocks, containing 858 and 550 individuals respectively. We observed more individuals travelling from the colony (2370) than towards it (1287) and this ratio varied between vantage points (1062:322, 401:643 and 907:322 at FN, IM and SA, respectively).

Immatures comprised 20% of 1012 commuting gannets. There was weak evidence that the proportion of immatures differed among outward and inward commuters (22 vs 16%;

pooled VPs: χ^2 (1,1012) = 3.78, p = 0.052). Most commuting gannets travelled in flocks (67% of 2249 individuals; median flock size = 3; range, 2–38 birds). This was true of both adults (61% travelled in flocks) and immatures (83% travelled in flocks). Single birds occurred more frequently than expected from a Poisson distribution (Fig. 1; score test (van den Broek 1995) $S(\beta)_1$ = 376, p < 0.001), suggesting that flock formation and flock size may have different drivers. Although adults comprised 80% of the population, they accounted for 88% of single birds, due to the fact that immatures were more likely to travel in flocks than adults (chi-squared test χ^2 (1,1012) = 20.83, p < 0.001). Flock size was unaffected by headwind speed (Supplementary material Appendix 1 Table A2) but flocks flying towards the colony were larger than those flying away from it (Table 2). A GLMM showed that the probability of gannets travelling in a flock, rather than alone, was best predicted by age (i.e. adult or immature), flight direction relative to the colony, headwind speed and two-way interactions between the latter (Table 3, Supplementary material Appendix 1 Table A3). Headwind speed ranged from −4.0 to 2.4 m s^{-1} (mean −0.6 m s^{-1}, SD 1.5 m s^{-1}). In zero headwinds, gannets travelling towards the colony were marginally more likely to do so in flocks than those travelling away from it (Fig. 2). Gannets flying towards the colony were more likely to do so in flocks as headwinds increased but the converse was true among birds flying away from the colony. This model confirmed that immatures were more likely to travel in flocks than adults, both when travelling towards and away from the colony. Fifty-three percent of 179 known-age flocks contained only adults, 8% only immatures and 40% both adults and immatures. These proportions differed from expected under the null hypothesis that individual identity was exchangeable (G-test G (2,179) = 25.30, p < 0.001; expected proportions 41, 3 and 56% respectively) – i.e. there was a slight tendency to flock with birds of a similar age, especially among adults.
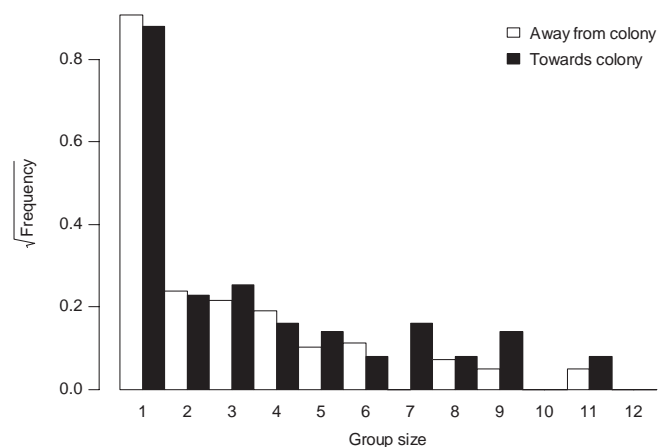

Figure 1. Size of groups of gannets travelling to and from the Bass Rock (note that in order to illustrate both the high frequency of groups of one and variation in the frequency distribution of group of > 1, frequency is square-root transformed).

Table 2. Negative binomial GLMM of the size of known-age flocks of gannets observed from land, travelling towards or away from Bass Rock (BR); n = 179 flocks, comprising adults, immatures or both).

Direction	Estimate	SE	t	p
Travelling away from BR	1.25	0.10	12.51	< 0.001
Travelling towards BR	0.23	0.09	2.59	0.010

Flock size is on the log scale. Steps in model selection are shown in Supplementary material Appendix 1 Table A2.

Eighty-seven percent of the 301 mixed-age flocks with observed age structure were led by adults (Fig. 3) – more than expected by chance (permutation test p < 0.001; median t_{perm} = 59.5%, CI [54.2–64.8]) but immatures followed adults no more frequently during outward than inward commutes in these flocks (chi-squared test χ^2 (1,301) = 0.15, p < 0.698). An immature occupied the last position in t_{obs} = 37.5% of 192 flocks that contained at least two mixed-age followers, which was no more frequent than expected by chance (permutation test p = 0.854; median t_{perm} = 41.1%, CI [34.9–47.9]). Mixed-age flocks most frequently comprised two birds – one adult and one immature (26% of 411 flocks). Adults led 88.5% of flocks comprising one adult and one immature for which flock order was recorded, more than expected by chance (chi-squared test χ^2 (1,78) = 51.60, p < 0.001) but the probability of the immature bird following in these flocks was not dependent on its age, its flight direction relative to the colony or headwind speed (Supplementary material Appendix 1 Table A4). The majority (t_{obs} = 70%) of the 20 mixed-immature flocks recorded with known age structure were led by the oldest flock member, but this effect was weak (permutation test p = 0.049; median t_{perm} = 50.0%, CI [30.0–70.0]).

Gannets observed at sea

Boat-based observations were made on 25 d during surveys, lasting between 3 and 11 h, and carried out between 06:14 and 16:46 GMT (Supplementary material Appendix 1 Table A1). Median Beaufort wind force during data collection was 2 (i.e. ~2–3 m s^{-1}; range Beaufort 0–4). A total of 64 mixed-age and six mixed-immature flocks were recorded, comprising 197 and 14 individuals, respectively (Fig. 3). The proportions of birds

Table 3. Binomial GLMM of the proportion of gannets (n = 1012) travelling in flocks when observed from land in the vicinity of Bass Rock (BR).

Covariate	Estimate	SE	z	p
Intercept	0.95	0.34	2.75	0.006
Direction (towards BR)	0.24	0.21	1.16	0.247
Headwind	−0.23	0.06	3.79	< 0.001
Age (immature)	0.49	0.20	2.47	0.014
Direction (towards BR) × headwind	0.42	0.11	−3.73	< 0.001

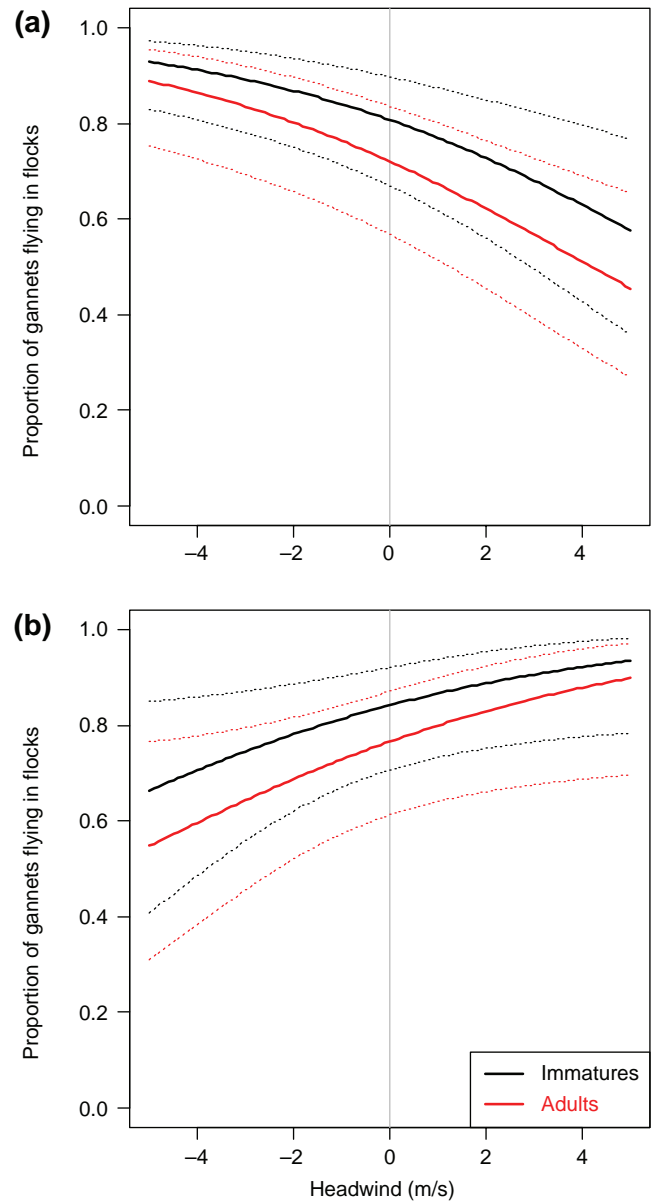Steps in model selection are shown in Supplementary material Appendix 1 Table A3.

Figure 2. Mean proportion of gannets observed in the vicinity of Bass Rock travelling in flocks rather than alone versus headwind speed (Table 2). Birds travelling (a) away from the colony and (b) towards it. Dashed lines indicate approximate 95% CIs.

of each age class in these flocks did not differ from those in flocks observed from land (chi-squared test χ^2 (4,1619) = 7.89, p = 0.062). As with flocks observed from land, more mixed-age flocks observed at sea were led by adults (t_{obs} = 89% of 64 flocks) than expected by chance (permutation test p < 0.001; median t_{perm} = 51.6% CI [40.6–64.1], Fig. 3). An immature occupied the last position in t_{obs} = 30.0% of 20 flocks that contained at least two mixed-age followers, which was no more frequent than expected by chance (permutation test p = 0.537; median t_{perm} = 35%, CI [15–55]). There were insufficient data (n = 6) to test whether mixed-immature flocks were led by the oldest bird. As with flocks observed from land, the majority
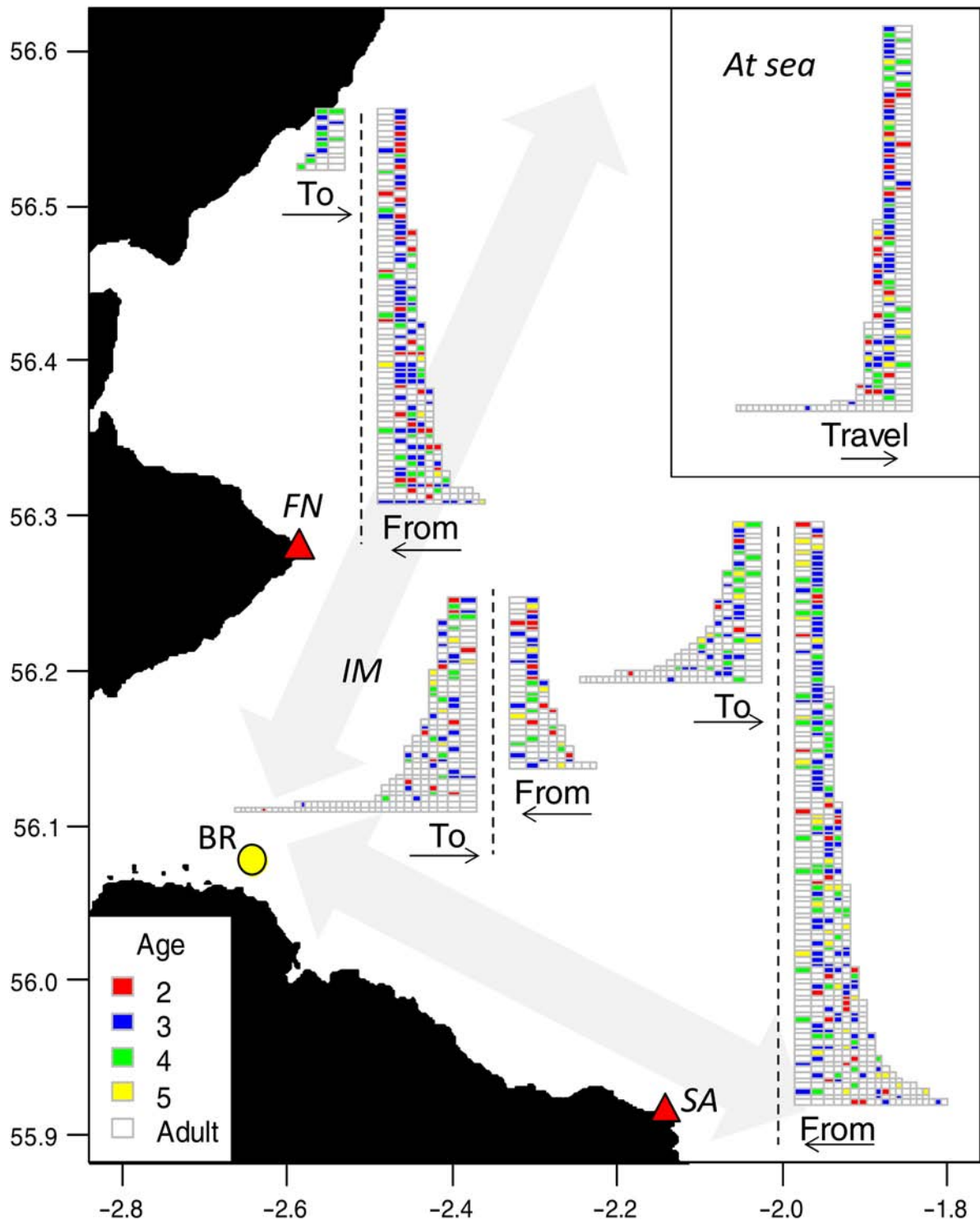
Figure 3. Mixed-age flocks of gannets travelling to and from Bass Rock (BR) during the breeding season are led more frequently by adults (white boxes) than immatures (coloured boxes). Each row corresponds to a flock recorded from the nearest land-based vantage point (red triangles: FN, Fife Ness; IM, Isle of May; SA, St Abbs Head). Black arrows indicate the travel direction of flocks (to/from BR) and large grey arrows the main flight paths of foraging adults commuting to and from BR (Hamer et al. 2000, Wakefield et al. 2013, 2015). Inset: mixed-age gannet flocks in direct flight recorded from boats offshore.

(47%) of mixed-age flocks comprised one adult and one immature and the majority (87%) of these flocks were led by the adult – more than expected by chance (chi-squared test χ^2 (1,30) = 16.13, p < 0.001). Again, the probability of immatures following in these flocks was unaffected by their age (LRT full vs intercept-only model χ^2 (1) = 0.03, p = 0.865).

7

Morphology and theoretical flight performance

The masses and wing spans of immature gannets did not differ from those of adults, but immatures had wider wings, and lower aspect ratios and wing loadings than adults (Table 4). Predicted V_{ms} was 0.5 m s^{-1} greater for adults than immatures but age differences for other predicted optimal airspeeds were slight and weakly supported.

Discussion

We found that the frequency of flocking and flock size among commuting gannets were largely consistent with group travel performing an aerodynamic function (Table 1). However, immatures were more likely to travel in flocks than adults and adults occurred at the front of mixed-age flocks more frequently than expected by chance. The latter behaviour was evident both in flocks observed near a large colony and among those travelling over the open sea, far from land. Below, we consider whether this could be because immatures are slower, for example due to morphological differences or whether immatures could follow adults in order to locate prey.

Aerodynamic and geometric effects on flock size

Commuting flocks of gannets typically adopt 'V' or echelon formations (Nelson 2001). This suggests that flocks form, in part at least, as a result of individuals following one another to reduce energetic costs (Lissaman and Shollenberger 1970, Weimerskirch et al. 2001, Voelkl et al. 2015). If gannets travel in flocks for aerodynamic reasons, we would expect birds returning to the colony to travel in flocks more frequently (and in larger flocks) than those commuting away from the colony (prediction 1), which is indeed what we found. A similar effect was noted in a study conducted at sea near the Bass Rock (Camphuysen 2011). We envisage that the difference in flock size results in part due to central-place geometry: travelling in a group to save energy is only advantageous if all group members share the same goal or at least intend to travel part of the journey in the same direction (Voelkl et al. 2015). Multi-year tracking has shown that although gannets from the Bass Rock forage most frequently to the northeast or southeast of the colony, birds radiate from the colony in most directions (Hamer et al. 2000, 2009, Wakefield et al. 2015, Grecian et al. 2018). Moreover, adults tend to forage in individually favoured but spatially disparate locations (Wakefield et al. 2015). As such, the courses of outward commuting birds will tend to diverge. In contrast, those of returning birds must clearly converge on the colony. Hence, it would be patent to inward commuters that conspecifics travelling in broadly the same direction as themselves shared the same goal, so travelling with them would be low risk. Conversely, it would be much less certain to outward commuters whether conspecifics were travelling to their intended destination, making joining them higher risk.

We additionally expected that if gannets travelled in flocks to save energy, they would do so more frequently when encountering headwinds (prediction 2). This was the case among birds travelling towards the colony but not away from it. It is unclear from our data why this should be but three potential explanations present themselves: firstly, northern gannets returning to the colony from foraging trips are ~0.7 kg heavier on average than those departing it (Lewis et al. 2004). Energetic expenditure during flight scales with body mass (Pennycuick 1978, Schmidt-Wellenburg et al. 2008), therefore returning birds may be more likely to seek to reduce aerodynamic costs during headwind flight by travelling in flocks. Secondly, flight and foraging are energetically more demanding than resting on the sea or in the colony (Birt-Friesen et al. 1989, Green et al. 2009). Birds approaching the colony at the end of return commutes may therefore be more fatigued than those that have just departed on outward flights, again making them more prone to seek to reduce aerodynamic costs. Finally, we note that birds travelling from the Bass Rock tend to pass closer to land than those travelling towards it, an effect that is also apparent, but not hitherto remarked upon, from tracking data (Wakefield et al. 2015, Grecian et al. 2018). We noticed that gannet flocks tend to become fragmented as they round promontories. This may result from individuals seeking to reduce headwinds by flying in the area of horizontal wind shear associated with cliffs. Turbulence in this boundary layer could make coordination among individuals difficult, resulting in the breakup of flocks and the observed negative relationship between flocking and headwind speed. Ultimately, biologging techniques, for example using bird borne cameras, GPS units and accelerometers,

Table 4. Morphology and theoretical flight performance of immature and adult gannets.

Parameter	Immature (n = 26)	Adult (n = 21)	t-statistic	p
Mass (kg)	2.85 ± 0.22	2.92 ± 0.22	−1.08	0.286
Wing span (mm)	1.831 ± 0.031	1.831 ± 0.040	−0.07	0.946
Wing area (m²)	0.237 ± 0.012	0.225 ± 0.012	3.45	< 0.001
Aspect ratio	14.2 ± 0.7	15.0 ± 0.8	−3.77	< 0.001
Wing loading (N(m²)$^{-1}$)	118 ± 11	128 ± 13	−2.72	0.009
V_{ms} (m s^{-1})	10.3 ± 0.5	10.8 ± 0.5	−2.73	0.009
V_{bg} (m s^{-1})	14.2 ± 0.5	14.4 ± 0.5	−1.61	0.114
V_{mp} (m s^{-1})	14.8 ± 0.4	15.0 ± 0.4	−1.04	0.304
V_{mr} (m s^{-1})	22.4 ± 0.6	22.5 ± 0.6	−0.27	0.786

V_{ms} = minimum sink speed; V_{bg} = best glide speed; V_{ms} = minimum power speed; V_{mr} = maximum range speed.

may be better able to resolve these effects than land-based observations (Yoda et al. 2004, Ropert-Coudert et al. 2006, Amélineau et al. 2014).

Speed and motivation as drivers of flock position

When flying in formation for aerodynamic reasons, birds are expected to match the amount of time they spend leading and following one another (Voelkl et al. 2015). Clearly this was not the case in the mixed-age gannet flocks that we observed, because adults led disproportionately. An additional mechanism, either aerodynamic or behavioural, must therefore explain our finding that gannet flocks are structured by age. One potential explanation is that immatures fly more slowly than adults (Herbert-Read 2016) – that is, immatures could be 'obligate followers'. For example, among both pigeons and roach *Rutilus rutilus*, the largest, fastest individuals occupy lead positions in travelling groups (Krause et al. 1998, Pettit et al. 2015). We examined this possibility, firstly by calculating the optimal flight speeds of gannets, which are dependent on mass and wing shape (Pennycuick 2008). We found that mass and wing length of gannets differed little between age classes, but adults had wider wings, with lower aspect ratios than immatures (Table 3). As a result, adults have faster theoretical minimum sink speeds ($V_{ms} = 10.8$ vs 10.3 m s^{-1}). However, while V_{ms} is optimal in soaring flight (Pennycuick 2008), the vast majority of gannets recorded during our study flew by flap-gliding (93%) or flapping (6%) – i.e. a mixture of powered and soaring flight (< 1% used purely soaring flight). In powered flight, it is optimal to fly at or below the minimum power speed V_{mp} (Pennycuick 1997, 2008). The typical speed of commuting gannets is 15–16 m s^{-1} (Pennycuick 1997), much closer to V_{mp} (15.0 m s^{-1}) then V_{ms} (10.8 m s^{-1}; Table 3). The difference between immature and adult V_{mp} predicted in our study was slight (14.8 vs 15.0 m s^{-1}), suggesting that morphologically mediated differences in flight speed (prediction 7) are unlikely to account for adults leading mixed-age flocks.

Conceivably, other differences in flight performance could account for adults leading mixed-age flocks. For example, differences in the flapping activity of GPS-tracked juvenile white storks *Ciconia ciconia* are not necessarily due to morphology but may relate to inexperience (Flack et al. 2018). Similarly, immature gannets could fly more slowly due to poorly developed flight skills. However, flight proficiency is apparently gained in the first few months post fledging in closely related brown boobies (Yoda et al. 2004, Kohno and Yoda 2011). The immatures observed in our study were a year or more old, and therefore would have successfully completed at least one winter migration prior to our study, in the majority of cases to northwest Africa and back (Nelson 2001). As such, they were probably as proficient in flight as adults.

Finally, in some species, the individuals most motivated to feed travel at the front of groups (Conradt et al. 2009, Herbert-Read 2016). Adult and immature gannets foraging from the Bass Rock spend a similar proportion of trips foraging but adults' trip durations are shorter (Grecian et al.

2018), possibly because they are more time-constrained and therefore need to commute more rapidly. However, if immatures are slower for any of the reasons discussed above, or less motivated than adults due to lower energetic demands, then not only should they occur less frequently than expected at the front of mixed-age flocks, but they should also occur more frequently in the last position (prediction 8). Contrary to this prediction, we found that the age of birds occupying the last position in mixed-age flocks was no different to that expected by chance, so we tentatively conclude that obligate following by immatures is unlikely to be the main cause of adults leading flocks disproportionately. In future studies, possible effects of individual flight performance on flock position could be tested using bird-borne telemetry, such as GPS tracking, accelerometery and camera loggers (Yoda et al. 2004, 2011, Flack et al. 2018). These techniques, combined with supplemental feeding of adults and/or offspring, could also perhaps be used to test whether motivation affects flock leadership, or indeed the propensity to travel in groups in the first place (Hansen et al. 2015).

Information gathering as a driver of flock position

In the previous section we argued that age-related asymmetries in flight performance or motivation are unlikely to fully explain why adults lead mixed-age flocks more frequently than expected by chance (predictions 7 and 8). As far as we are aware, the only remaining alternative explanation is that immatures follow adults in order to locate prey. This result is therefore consistent with both the information centre hypothesis (Ward and Zahavi 1973), and the hypothesis that at-sea spatial segregation among gannet colonies is mediated through public information exchange (Grémillet et al. 2004, Wakefield et al. 2013). However, we caution that we tested neither hypothesis directly. Rather, we simply show for the first time, that one group of birds assumed to be less well informed about the location of prey (immatures) systematically follow another group (adults) that are assumed to be better informed (prediction 5). Given that the true level of experience of individuals recorded in our study was unknown, the validity of this assumption deserves further consideration: most immature gannets from the Bass Rock migrate out of the North Sea very soon after fledging and only return in their second or third summers (Nelson 2001). On returning, they may visit multiple colonies before beginning to carry our central-place foraging trips from one colony (Votier et al. 2011, 2017). Hence, the majority of the immatures that we recorded would have had little time to explore and learn the distribution of potential foraging areas relative to Bass Rock, which extend to > 1 million km^2 (Wakefield et al. 2013). The assumption that immatures are less knowledgeable than adults is further supported by the fact that breeding northern gannets generally return repeatedly to individually-specific foraging areas only 10s–100s km^2 in extent (Hamer et al. 2000, Patrick et al. 2014, Wakefield et al. 2015), whereas immatures usually forage in different locations on each successive trip (Votier et al. 2017, Grecian et al. 2018). This

9

implies that adults use memory as a foraging cue, whereas immatures are necessarily more exploratory (Votier et al. 2017). Notwithstanding these points, it is important to recall that we used plumage characteristics as a proxy for experience. Given that all gannets older than five years have essentially the same plumage, we could not discriminate between younger (less experienced) and older (more experienced) adults. Although this would have decreased the precision of our models it should not have biased them. Moreover, we presume that gannets themselves are only able to discriminate the relative experience of conspecifics seen at sea from their plumage, making the use of plumage as a proxy for informedness appropriate for our study.

If immatures do follow adults from the colony, how might this occur? Immatures form large aggregations at colony edges during the breeding season (Nelson 2001). We did not observe the formation of flocks, but departing flocks were already structured by age at our closest observation point, 13 km from the colony. Hence, immatures must begin to follow older birds either in or near the colony, perhaps by first joining them in social rafts (Machovsky-Capuska et al. 2013, Thiebault et al. 2014a) or from the gyres of soaring birds that we have often noted near colonies. Our observations at sea show that flocks were also age-structured remote from land. While it cannot be concluded from this that immatures follow older birds all the way to foraging areas, GPS tracking has recently shown that Australasian gannets leaving a small colony at the same time had more similar initial destinations than individuals leaving at different times, suggesting that birds commute from colonies to foraging patches together (Jones et al. 2018). Although this result could also arise due to individuals using the same cues to locate distant foraging patches, tracking has shown that immature gannets often take direct rather than circuitous paths to foraging areas (Votier et al. 2017). It is difficult to envisage how naïve birds could fly directly between the colony and different foraging areas on each successive trip without doing so by following more informed individuals at least some of the time. Together with evidence implying that gannets use memory extensively as a foraging cue during adulthood (see below), our results therefore lend weight to the hypothesis that the public information use required to mediate among-colony spatial segregation occurs most frequently during immaturity (Wakefield et al. 2015). In the future, bird-borne cameras could be used to test this supposition more rigorously (Yoda et al. 2011, Tremblay et al. 2014).

A result that is not easy to reconcile with the hypothesis that following occurs due to information seeking is that immatures also followed adults disproportionately when returning to the colony. Gannets visit multiple colonies during immaturity (Votier et al. 2011), so immatures may occasionally follow inward commuting adults to locate new colonies. Similarly, immatures already attending the Bass Rock could follow adults in order to relocate the colony after foraging trips. This may be necessary because immatures tend to visit different foraging locations on successive foraging trips and so must often be faced with the navigational challenge of returning to the colony from an unfamiliar location. Alternatively, the propensity to follow adults may be rather insensitive to context during immaturity. This could be adaptive, if, for example, immatures also benefit from following adults during migration.

A social learning hypothesis of seabird foraging

It has long been suggested that delayed maturation (up to 10 yr in some species) is an adaptation to allow seabirds to learn to subsist on the widely and patchily dispersed prey typical of pelagic environments (Lack 1968). Foraging ontogenesis has been demonstrated in a number of seabird species (Orians 1969, Kohno and Yoda 2011, Riotte-Lambert and Weimerskirch 2013). It has recently been hypothesised that seabirds learn foraging patches though a process of exploration and refinement (Guilford et al. 2011). If correct, exploration could occur purely on an individual level but theory suggests it would be more efficient to additionally use public information as a guide (Galef and Whiskin 2004, Guttal and Couzin 2010). Hence, our results lead us to hypothesise that immature gannets learn in part by following adults – what we refer to as the 'social learning hypothesis', which can be seen as an extension of the 'exploration-refinement hypothesis' of seabird foraging (Guilford et al. 2011). Social learning of this type – when relatively naïve animals follow more experienced ones – is increasingly recognized as an important mechanism in the ontogenesis of movement and foraging strategies (Hoppitt and Laland 2013). For example, immature whooping cranes learn migratory routes more rapidly if they travel with older birds (Mueller et al. 2013); reintroduced bighorn sheep are initially sedentary but become migratory with time due to social learning (Jesmer et al. 2018); older, more experienced, pigeons usually lead mixed-age flocks (Flack et al. 2012, Jorge and Marques 2012); and naïve guppies *Poecilia reticulata* learn to locate food patches by following more experienced conspecifics (Laland and Williams 1997). In support of the social learning hypothesis, we found that within mixed-age flocks of subadults, the oldest birds were most likely to lead (prediction 6), which would be consistent with a gradual accrual of information during immaturity (Riotte-Lambert and Weimerskirch 2013). Similar behaviour may occur among other sulids. Using bird-borne cameras, Yoda et al. (2011) showed that while immature brown boobies *Sula leucogaster* follow both immature and adult conspecifics, they follow the latter for much longer.

Some features that gannets forage in association with are inherently static e.g. bathymetrically-tied fronts (Wakefield et al. 2015) but climatic fluctuations, trophodynamics, etc. can give rise to macroscale (100s km) changes in the distribution of prey (Weijerman et al. 2005, Carroll et al. 2015). It is likely therefore that gannets also learn through personal exploration, perhaps explaining in part why 17% of immatures observed in our study travelled alone. At finer spatiotemporal scales prey are less predictable and must therefore be detected through personal exploration or network foraging/local enhancement (Wittenburger and Hunt 1985). For example, Cape gannets

are able to detect and respond to aggregations of foraging conspecifics up to 40 km distant, with reaction distances increasing with aggregation size (Thiebault et al. 2014b). Ultimately, the use of such public information is predicted to be most effective in predictable or semi-predictable environments (Galef and Whiskin 2004, Guttal and Couzin 2010).

A potential objection to the hypothesis that immature gannets follow adults to gain information is that any cost to adults due to this behaviour could provide a selective pressure against its continuance. An obvious potential cost to adults from being followed is that they would suffer greater competition on arrival at a prey patch. However, this does not seem to be the case. In fact, the prey capture rates of Cape gannets actually increase in the presence of conspecifics, due to facilitation (Thiebault et al. 2016). Another potential cost to adults of being followed is that within V and echelon-shaped flocks, it is energetically more costly to fly in the lead position (Weimerskirch et al. 2001). Flocks of northern bald ibises *Geronticus eremita* flying in these formations remain cohesive only if individuals reciprocate by taking equal turns leading and following (Voelkl et al. 2015). The tendency of immatures to follow adults may therefore reduce flock cohesion. This could perhaps explain why we found that adults were slightly more likely than expected to form flocks with other adults, than with immatures. That is, adults may prefer to join flocks of other adults than flocks containing immatures, because the former are more likely to reciprocate than the latter. Even if this were the case however, flying in a mixed-age flock in which at least some of the other flock members reciprocate in taking the front position would be energetically more advantageous to adults than travelling alone (Lissaman and Shollenberger 1970). Indeed, when one adult is followed by one immature (which we observed frequently), being followed would be no more energetically costly than travelling alone, whereas attempting to evade being followed could be very costly (Herbert-Read et al. 2013).

As a coda, we note that although we hypothesise that immatures follow adults to facilitate social learning, it is conceivable that the direction of causality is opposite. That is, if immatures are indeed slower than adults due to their morphology, locomotive proficiency, motivation, etc., information on foraging locations would still tend to flow from older to younger birds, with social learning occurring as an inevitable consequence of obligate following. Immature (naïve) animals are often smaller and therefore slower than older (more experienced) conspecifics. Travel in mixed-age groups may therefore inevitably give rise to passive social learning through following in many taxa and the emergence of group-level phenomena, such as traditional foraging areas, may be more dependent on biomechanics than is usually acknowledged (Galef and Giraldeau 2001, Hoppitt and Laland 2013).

Conclusions

We hypothesised that gannets travel in flocks to reduce flight costs and that young gannets follow older ones in order to locate prey. Although we observed flock structures consistent with both hypotheses, neither was fully supported by our results. In particular, adults led inward commuting flocks as frequently as outward commuting flocks, which is inconsistent with the information centre hypothesis. Nonetheless, the fact that adults systematically fly at the front of mixed age flocks was unambiguous. Biologging methods could perhaps confirm whether adults lead immatures all the way to foraging locations. If they do, the resultant flow of information from adults to immatures would have important implications for our understanding of colonial living among central-place foragers.

References

Alerstam, T., Rosén, M., Bäckman, J., Ericson, P. G. P. and Hellgren, O. 2007. Flight speeds among bird species: allometric and phylogenetic effects. – PLoS Biol. 5: e197.

Alexander, R. D. 1974. The evolution of social behavior. – Annu. Rev. Ecol. Syst. 5: 325–383.

Amélineau, F., Péron, C., Lescroël, A., Authier, M., Provost, P. and Grémillet, D. 2014. Windscape and tortuosity shape the flight costs of northern gannets. – J. Exp. Biol. 217: 876–885.

Barrett, R. T. 2008. Recent establishments and extinctions of northern gannet *Morus bassanus* colonies in North Norway, 1995–2008. – Ornis Norveg. 31: 172–182.

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

Birt-Friesen, V. L., Montevecchi, W. A., Cairns, D. K. and Macko, S. A. 1989. Activity-specific metabolic rates of free-living northern gannets and other seabirds. – Ecology 70: 357–367.

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. and White, J. S. S. 2009. Generalized linear mixed models: a practical guide for ecology and evolution. – Trends Ecol. Evol. 24: 127–135.

Brown, C. R. and Brown, M. B. 2001. Avian coloniality. – In: Nolan, V. and Thompson, C. F. (eds), Current ornithology. Springer, pp. 1–82.

Camphuysen, C. J. 2011. Northern gannets in the North Sea: foraging distribution and feeding techniques around the Bass Rock. – Brit. Birds 104: 60–76.

Camphuysen, C. J., Fox, T., Leopold, M. F. and Petersen, I. K. 2004. Towards standardised seabirds at sea census techniques in

connection with environmental impact assessments for offshore wind farms in the UK [COWRIE BAM-02-2002]. – Crown Estate, London, p. 38.

Carroll, M. J., Butler, A., Owen, E., Ewing, S. R., Cole, T., Green, J. A., Soanes, L. M., Arnould, J. P. Y., Newton, S. F., Baer, J., Daunt, F., Wanless, S., Newell, M. A., Robertson, G. S., Mavor, R. A. and Bolton, M. 2015. Effects of sea temperature and stratification changes on seabird breeding success. – Clim. Res. 66: 75–89.

Cleasby, I. R., Wakefield, E. D., Bearhop, S., Bodey, T. W., Votier, S. C. and Hamer, K. C. 2015. Three-dimensional tracking of a wide-ranging marine predator: flight heights and vulnerability to offshore wind farms. – J. Appl. Ecol. 52: 1474–1482.

Conradt, L., Krause, J., Couzin, I. D. and Roper, T. J. 2009. 'Leading according to need' in self-organizing groups. – Am. Nat. 173: 304–312.

Dall, S. R. X., Giraldeau, L. A., Olsson, O., Mcnamara, J. M. and Stephens, D. W. 2005. Information and its use by animals in evolutionary ecology. – Trends Ecol. Evol. 20: 187–193.

Edgington, E. and Onghena, P. 2007. Randomization tests. – Chapman and Hall.

Flack, A., Pettit, B., Freeman, R., Guilford, T. and Biro, D. 2012. What are leaders made of? The role of individual experience in determining leader-follower relations in homing pigeons. – Anim. Behav. 83: 703–709.

Flack, A., Nagy, M., Fiedler, W., Couzin, I. D. and Wikelski, M. 2018. From local collective behavior to global migratory patterns in white storks. – Science 360: 911–914.

Galef, B. G. and Giraldeau, L. A. 2001. Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. – Anim. Behav. 61: 3–15.

Galef, B. G. and Whiskin, E. E. 2004. Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. – Anim. Behav. 68: 897–902.

Grecian, W. J., Lane, J. V., Michelot, T., Wade, H. M. and Hamer, K. C. 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. Interf. 15: 20180084.

Green, J. A., White, C. R., Bunce, A., Frappell, P. B. and Butler, P. J. 2009. Energetic consequences of plunge diving in gannets. – Endang. Species Res. 10: 269–279.

Grémillet, D., Dell'omo, G., Ryan, P. G., Peters, G., Ropert-Coudert, Y. and Weeks, S. J. 2004. Offshore diplomacy, or how seabirds mitigate intra-specific competition: a case study based on GPS tracking of Cape gannets from neighbouring colonies. – Mar. Ecol. Prog. Ser. 268: 265–279.

Guilford, T., Freeman, R., Boyle, D., Dean, B., Kirk, H., Phillips, R. and Perrins, C. 2011. A dispersive migration in the Atlantic puffin and its implications for migratory navigation. – PLoS One 6: e21336.

Guttal, V. and Couzin, I. D. 2010. Social interactions, information use and the evolution of collective migration. – Proc. Natl Acad. Sci. USA 107: 16172–16177.

Hamer, K. C., Phillips, R. A., Wanless, S., Harris, M. P. and Wood, A. G. 2000. Foraging ranges, diets and feeding locations of gannets *Morus bassanus* in the North Sea: evidence from satellite telemetry. – Mar. Ecol. Prog. Ser. 200: 257–264.

Hamer, K. C., Humphreys, E. M., Magalhães, M. C., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Skov, H. and Wanless, S. 2009. Fine-scale foraging behaviour of a medium-ranging marine predator. – J. Anim. Ecol. 78: 880–889.

Hansen, M. J., Schaerf, T. M. and Ward, A. J. W. 2015. The influence of nutritional state on individual and group movement behaviour in shoals of crimson-spotted rainbowfish (*Melanotaenia duboulayi*). – Behav. Ecol. Sociobiol. 69: 1713–1722.

Hartig, F. 2018. DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. – R package ver. 0.2.0, <https://CRAN.R-project.org/package=DHARMa>.

Heinemann, D. 1981. A range finder for pelagic bird censusing. – J. Wildl. Manage. 45: 489–493.

Herbert-Read, J. E. 2016. Understanding how animal groups achieve coordinated movement. – J. Exp. Biol. 219: 2971–2983.

Herbert-Read, J. E., Krause, S., Morrell, L. J., Schaerf, T. M., Krause, J. and Ward, A. J. W. 2013. The role of individuality in collective group movement. – Proc. R. Soc. B 280: 20122564.

Hoppitt, W. and Laland, K. N. 2013. Social learning: a introduction to mechanisms, methods and models. – Princeton Univ. Press.

Jesmer, B. R., Merkle, J. A., Goheen, J. R., Aikens, E. O., Beck, J. L., Courtemanch, A. B., Hurley, M. A., Mcwhirter, D. E., Miyasaki, H. M., Monteith, K. L. and Kauffman, M. J. 2018. Is ungulate migration culturally transmitted? Evidence of social learning from translocated animals. – Science 361: 1023–1025.

Jones, T. B., Patrick, S. C., Arnould, J. P. Y., Rodríguez-Malagón, M. A., Wells, M. R. and Green, J. A. 2018. Evidence of sociality in the timing and location of foraging in a colonial seabird. – Biol. Lett. 14: 20180214.

Jorge, P. E. and Marques, P. A. M. 2012. Decision-making in pigeon flocks: a democratic view of leadership. – J. Exp. Biol. 215: 2414–2417.

Kohno, H. and Yoda, K. 2011. The development of activity ranges in juvenile brown boobies *Sula leucogaster*. – Ibis 153: 611–615.

Krause, J., Reeves, P. and Hoare, D. 1998. Positioning behaviour in roach shoals: the role of body length and nutritional state. – Behaviour 135: 1031–1039.

Lack, D. 1968. Ecological adaptations for breeding in birds. – Methuen, London.

Laland, K. N. and Williams, K. 1997. Shoaling generates social learning of foraging information in guppies. – Anim. Behav. 53: 1161–1169.

Lewis, S., Hamer, K., Money, L., Griffiths, R., Wanless, S. and Sherratt, T. 2004. Brood neglect and contingent foraging behavior in a pelagic seabird. – Behav. Ecol. Sociobiol. 56: 81–88.

Lissaman, P. B. and Shollenberger, C. A. 1970. Formation flight of birds. – Science 168: 1003–1005.

Machovsky-Capuska, G., Hauber, M., Libby, E., Amiot, C. and Raubenheimer, D. 2013. The contribution of private and public information in foraging by Australasian gannets. – Anim. Cognit. 1–10.

Marzluff, J. M., Heinrich, B. and Marzluff, C. S. 1996. Raven roosts are mobile information centres. – Anim. Behav. 51: 89–103.

Mueller, T., O'Hara, R. B., Converse, S. J., Urbanek, R. P. and Fagan, W. F. 2013. Social learning of migratory performance. – Science 341: 999–1002.

Murray, S., Wanless, S. and Harris, M. P. 2014. The Bass Rock – now the world's largest northern gannet colony. – Brit. Birds 107: 765–769.

Nelson, B. 2001. The Atlantic gannet. – Fenix Books Ltd, Great Yarmouth.

Nelson, B. 2006. Pelicans, cormorants and their relatives. – Oxord Univ. Press.

Orians, G. H. 1969. Age and hunting success in the brown pelican (*Pelecanus occidentalis*). – Anim. Behav. 17: 316–319.

Patrick, S. C., Bearhop, S., Grémillet, D., Lescroël, A., Grecian, J. W., Bodey, T. W., Hamer, K. C., Wakefield, E. D., Le Nuz, M. and Votier, S. C. 2014. Individual foraging specialisation and differences in searching behaviour of a wide-ranging marine predator. – Oikos 123: 33–40.

Pennycuick, C. 1997. Actual and 'optimum' flight speeds: field data reassessed. – J. Exp. Biol. 200: 2355–2361.

Pennycuick, C. J. 1978. Fifteen testable predictions about bird flight. – Oikos 30: 165–176.

Pennycuick, C. J. 1982. The flight of petrels and albatrosses (Procellariiformes), observed in South Georgia and its vicinity. – Phil. Trans. R. Soc. B 300: 75–106.

Pennycuick, C. J. 1989. Bird flight performance a practical calculation manual. – Oxford Univ. Press.

Pennycuick, C. J. 2008. Modelling the flying bird. – Elsevier.

Pettit, B., Ákos, Z., Vicsek, T. and Biro, D. 2015. Speed determines leadership and leadership determines learning during pigeon flocking. – Curr. Biol. 25: 3132–3137.

Portugal, S. J., Hubel, T. Y., Fritz, J., Heese, S., Trobe, D., Voelkl, B., Hailes, S., Wilson, A. M. and Usherwood, J. R. 2014. Upwash exploitation and downwash avoidance by flap phasing in ibis formation flight. – Nature 505: 399–402.

Riotte-Lambert, L. and Weimerskirch, H. 2013. Do naive juvenile seabirds forage differently from adults? – Proc. R. Soc. B 280: 20131434.

Ropert-Coudert, Y., Wilson, R. P., Gremillet, D., Kato, A., Lewis, S. and Ryan, P. G. 2006. Electrocardiogram recordings in free-ranging gannets reveal minimum difference in heart rate during flapping versus gliding flight. – Mar. Ecol. Prog. Ser. 328: 275–284.

Schmidt-Wellenburg, C. A., Engel, S. and Visser, G. H. 2008. Energy expenditure during flight in relation to body mass: effects of natural increases in mass and artificial load in Rose Coloured Starlings. – J. Comp. Physiol. B 178: 767–777.

Thiebault, A., Mullers, R., Pistorius, P., Meza-Torres, M. A., Dubroca, L., Green, D. and Tremblay, Y. 2014a. From colony to first patch: processes of prey searching and social information in Cape Gannets. –Auk 595–609.

Thiebault, A., Mullers, R. H. E., Pistorius, P. A. and Tremblay, Y. 2014b. Local enhancement in a seabird: reaction distances and foraging consequence of predator aggregations. – Behav. Ecol. 25: 1303–1310.

Thiebault, A., Semeria, M., Lett, C. and Tremblay, Y. 2016. How to capture fish in a school? Effect of successive predator attacks on seabird feeding success. – J. Anim. Ecol. 85: 157–167.

Tremblay, Y., Thiebault, A., Mullers, R. and Pistorius, P. 2014. Bird-borne video-cameras show that seabird movement patterns relate to previously unrevealed proximate environment, not prey. – PLoS One 9: e88424.

UK Meteorological Office 2018. MIDAS land surface stations data (1853–current). – British Atmospheric Data Centre006. Available from <http://badc.nerc.ac.uk/data/ukmo-mida>.

Van Den Broek, J. 1995. A score test for zero inflation in a Poisson distribution. – Biometrics 51: 738–743.

Voelkl, B., Portugal, S. J., Unsöld, M., Usherwood, J. R., Wilson, A. M. and Fritz, J. 2015. Matching times of leading and following suggest cooperation through direct reciprocity during V-formation flight in ibis. – Proc. Natl Acad. Sci. USA 112: 2115–2120.

Votier, S. C., Grecian, W. J., Patrick, S. and Newton, J. 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable isotope analysis. – Mar. Biol. 158: 355–362.

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

Wakefield, E. D., Bodey, T. W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R. G., Green, J. A., Grémillet, D., Jackson, A. L., Jessopp, M. J., Kane, A., Langston, R. H. W., Lescroël, A., Murray, S., Le Nuz, M., Patrick, S. C., Péron, C., Soanes, L. M., Wanless, S., Votier, S. C. and Hamer, K. C. 2013. Space partitioning without territoriality in gannets. – Science 341: 68–70.

Wakefield, E. D., Cleasby, I. R., Bearhop, S., Bodey, T. W., Davies, R., Miller, P., Newton, J., Votier, S. and Hamer, K. C. 2015. Long-term individual foraging site fidelity – why some gannets don't change their spots. – Ecology 96: 3058–3074.

Wakefield, E. D., Furness, R. W., Lane, J. V., Jeglinski, J. W. E. and Pinder, S. J. 2019. Data from: immature gannets follow adults in commuting flocks providing a potential mechanism for social learning. – Dryad Digital Repository, <http://dx.doi.org/10.5061/dryad.3rg5307>.

Ward, P. and Zahavi, A. 1973. Importance of certain assemblages of birds as information-centres for food-finding. – Ibis 115: 517–534.

Weijerman, M., Lindeboom, H. and Zuur, A. F. 2005. Regime shifts in marine ecosystems of the North Sea and Wadden Sea. – Mar. Ecol. Prog. Ser. 298: 21–39.

Weimerskirch, H., Martin, J., Clerquin, Y., Alexandre, P. and Jiraskova, S. 2001. Energy saving in flight formation – Pelicans flying in a 'V' can glide for extended periods using the other birds' air streams. – Nature 413: 697–698.

Weimerskirch, H., Bertrand, S., Silva, J., Marques, J. C. and Goya, E. 2010. Use of social information in seabirds: compass rafts indicate the heading of food patches. – PLoS One 5: e9928.

Wittenburger, J. F. and Hunt, G. L. J. 1985. The adaptive significance of coloniality in birds. – In: Farner, D. S., King, J. R. and Parkes, K. C. (eds), Avian biology. Academic Press, pp. 1–78.

Yoda, K., Kohno, H. and Naito, Y. 2004. Development of flight performance in the brown booby. – Proc. R. Soc. B 271: S240–S242.

Yoda, K., Murakoshi, M., Tsutsui, K. and Kohno, H. 2011. Social interactions of juvenile brown boobies at sea as observed with animal-borne video cameras. – PLoS One 6: e19602.

Supplementary material (available online as Appendix jav-02164 at <www.avianbiology.org/appendix/jav-02164>). Appendix 1.