



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



Annette L. Fayet^{a, *}, Robin Freeman^b, Akiko Shoji^a, Oliver Padget^a, Chris M. Perrins^c,
Tim Guilford^{a, *}

^a Oxford Navigation Group, Department of Zoology, University of Oxford, Oxford, U.K.

^b Institute of Zoology, Zoological Society of London, London, U.K.

^c Edward Grey Institute, Department of Zoology, University of Oxford, Oxford, U.K.

ARTICLE INFO

Article history:

Received 28 May 2015

Initial acceptance 9 July 2015

Final acceptance 17 August 2015

Available online

MS. number: 15-00454R

Keywords:

foraging efficiency

immature

intraspecific competition

spatial segregation

telemetry

Competition and, ultimately, adaptive specialization are the major ecological forces behind spatial segregation in foraging distributions, and are commonly driven by size-related differences in competitiveness between individuals of different sex, age or social status. However, such segregation can also be observed in long-lived monomorphic species, often between immature and breeding individuals. In many of these species, individuals often forage in patchy and potentially unpredictable environments in which resources can be spread over large scales and be difficult to find, and efficient foraging may require advanced cognitive skills (for example in navigation and memory). Particularly in species with deferred breeding, experience rather than size may be an important driver of segregation and may lead to differences in competitiveness between young and old, but whether there is a relationship between age, foraging efficiency and spatial segregation has never been properly investigated. Here we tested 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 ethoinformatics approach and mass gain. We found substantial spatial segregation between immature and breeding adults. Compared with adults, immatures gained less mass per unit of time spent foraging and foraged in less productive waters, suggesting lower foraging efficiency, probably because of inexperience.

© 2015 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Spatial segregation in foraging distributions driven by competition, which can eventually lead to adaptive specialization, is observed in a wide range of animal taxa, and often arises from size-related differences in competitiveness between individuals of different sex, age or social status (e.g. Durant, Kelly, & Caro, 2004; Gosler, 1987; Harcourt, Stewart, & Fossey, 1976; Webb, Marzluff, & Hepinstall-Cymerman, 2012). Long-lived animals with advanced cognitive capacities (vertebrates) may be able to exploit patchy, expansive and potentially unpredictable environments using individual memory and experience. This could provide a different mechanism driving spatial segregation, even in monomorphic species, if older, more experienced individuals

competitively displace younger cohorts through enhanced foraging efficiency. Higher adult foraging efficiency could result from two (not mutually exclusive) mechanisms: first, adults could have superior hunting skills, resulting in a higher food gain per unit of time spent foraging in areas of similar productivity; second, adults may exploit areas of higher productivity. Either hypothesis would lead to age-related differences in space use correlated with differences in foraging efficiency. Spatial segregation between immature (nonbreeding) and breeding adults during all or part of the year occurs in many species (e.g. primates: Harcourt et al., 1976; other mammals: Cheney & Seyfarth, 1983; Durant et al., 2004; Jarman, 1974; birds: Webb et al., 2012; insects: Robertson & Cushing, 2011). Immatures have been found to disperse more and cover larger ranges than breeders, although in some species they have been reported to undertake smaller-scale movements than adults (Field, Bradshaw, Burton, Sumner, & Hindell, 2005). Understanding such differences is of paramount importance when considering the

* Correspondence: A. L. Fayet and T. Guilford, Department of Zoology, University of Oxford, Oxford OX1 3PS, U.K.

E-mail addresses: annette.fayet@gmail.com (A. L. Fayet), tim.guilford@zoo.ox.ac.uk (T. Guilford).

demography of a species or its conservation needs. It has been suggested that spatial segregation between immature and adult individuals may be due to differences in foraging experience (Lack, 1954), and lower foraging efficiency has been documented in some species (Daunt, Afanasyev, Adam, Croxall, & Wanless, 2007; Lefebvre, 1995; Le Vaillant et al., 2012; Maclean, 1986). The relationship between efficiency and spatial segregation, however, has never been properly tested. Here we investigated this relationship in a long-lived pelagic seabird, the Manx shearwater, *Puffinus puffinus*. Pelagic seabirds, like many other marine animals, are long-lived, with a prolonged immature period. They forage in an open and patchy environment which can be unpredictable, depending on the type of marine habitat used and the spatial and temporal scales of their foraging trips (Weimerskirch, 2007). This may not only give them more opportunities to segregate, but also make learning and experience particularly important in the development of the skills necessary to forage effectively, for example to navigate to distant areas in a featureless environment, to identify and memorize 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 have attempted to do so, mainly because of the logistical challenges involved with tracking nonbreeding 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 larger range during nonbreeding (usually long-distance) movements in the winter (Clarke, Kerry, Fowler, Lawless, & Eberhard, 2003; Kooyman, Kooyman, Horning, & Kooyman, 1996; Kooyman & Ponganis, 2007; Pelletier, Chiaradia, Kato, & Ropert-Coudert, 2014; Péron & Grémillet, 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 (Péron & Grémillet, 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; 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 were too low to make any strong conclusion (Péron & Grémillet, 2013). Votier et al. (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 in 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 was our aim here.

Immature Manx shearwaters start to return to the colony in large numbers in their third year, and for 2–3 years spend over a month each summer regularly visiting the colony (Perrins et al., 1973). This makes them an ideal species to make simultaneous comparisons of the central-place foraging behaviour of immature

and breeding adults. In this study we investigated the relationship between efficiency and spatial segregation in Manx shearwaters by simultaneously tracking immature and breeding individuals with a mix of archival and remote-download GPS loggers. These allowed us to investigate potential spatial segregation while inferring individual foraging efficiency by combining an ethoinformatics 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). We also examined proxies of marine productivity for the areas in which birds foraged to determine whether any segregation was related to potential differences in habitat quality.

METHODS

Ethical Note

All work adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, and 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's Local Ethical Review Process. To minimize disturbance, handling was kept to a minimum (<10 min for each deployment/retrieval). Similar techniques and loggers have been deployed on adult Manx shearwaters in this colony since 2007 and no significant effect was recorded (Dean et al., 2012; Freeman et al., 2013). When possible, lighter devices were deployed on immatures: on average the devices represented an extra 0.4% (ca. 1.4 g) of the immatures' body mass compared with adults, less than the 5 g accuracy of our weight measurements and equivalent to or less than loads shown to have no significant short-term effect in closely related species (Iguar et al., 2004; Passos, Navarro, Giudici, & Gonzales-Solis, 2010). Therefore we are confident that our results are not biased by a greater impact on immatures. It was not possible to monitor the survival of immature birds as they do not return to a specific nest, but all adults had a breeding success similar to or higher than the rest of the colony after the experiment (Perrins et al. 2013–2014).

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 (ca. 300 000 breeding pairs; Perrins et al., 2012), in June–July 2013 and 2014. Manx shearwaters are ca. 400 g, 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.

Deployment of Devices

Since immatures appear similar to adults they were identified first by their behaviour on the surface, for example prolonged amounts of time on the surface, long periods of immobility, prospecting movements, no strong directional movement towards a particular burrow, quick exploration of many burrows (Brooke, 1990), and then, after being caught by hand, by the

Download English Version:

<https://daneshyari.com/en/article/8489508>

Download Persian Version:

<https://daneshyari.com/article/8489508>

[Daneshyari.com](https://daneshyari.com)