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Among-year and within-population variation in foraging distribution of European shags *Phalacrocorax aristotelis* over two decades: Implications for marine spatial planning

Maria I. Bogdanova [a,*], Sarah Wanless [a,*], Michael P. Harris [a], Jan Lindström [b], Adam Butler [c], Mark A. Newell [a], Katsufumi Sato [d], Yutaka Watanuki [e], Matt Parsons [f], Francis Daunt [a,*]

[a] Centre for Ecology & Hydrology, Bush Estate, Penicuik, Midlothian EH26 0QB, UK
[b] Institute of Biodiversity, Animal Health and Comparative Medicine, University of Glasgow, Graham Kerr Building, Glasgow G12 8QQ, UK
[c] Biomathematics & Statistics Scotland, JCMB, The King's Buildings, Edinburgh EH9 3JZ, UK
[d] International Coastal Research Center, Atmosphere and Ocean Research Institute, The University of Tokyo, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8564, Japan
[e] Graduate School of Fisheries Sciences, Hokkaido University, Minato-cho 3-1-1, Hakodate 041-8611, Japan
[f] Joint Nature Conservation Committee, Inverdee House, Baxter Street, Aberdeen AB11 9QA, UK

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A B S T R A C T

Marine spatial planning aims to deliver sustainable use of marine resources by minimizing environmental impacts of human activities and designating Marine Protected Areas. This poses a challenge where species' distributions show spatio-temporal heterogeneity. However, due to logistic constraints and challenging timescales many studies of distribution are undertaken over few years or on a restricted subset of the population. Long-term studies can help identify the degree of uncertainty in those less comprehensive in space and time. We quantify inter-annual and sub-colony variation in the summer foraging distribution of a population of European shags *Phalacrocorax aristotelis*, using a tracking data set comprising 320 individuals and 1106 foraging trips in 15 years from 1987 to 2010. Foraging distribution over the study period was concentrated in three areas. Data from one and two years captured an average of 54% and 64% of this distribution, respectively, but it required 8 years' data to capture over 90% of the distribution. Foraging range increased with population size when breeding success was low, suggesting interplay between extrinsic and intrinsic effects. Furthermore, females had foraging ranges on average 36% greater than males. Finally, sub-colony segregation occurred in foraging areas up to 4 km from the colony and in the most distant locations (>10 km), whilst there was considerable overlap at intermediate distances (6–10 km). Our study highlights important considerations for marine spatial planning in particular, and species conservation in general, notably the proportion of the population distribution identified, the prevailing conditions experienced and the need for balanced sampling across the population.

1. Introduction

The growing concern about the negative effects of human activities on marine wildlife underpins the goals of marine spatial planning, whereby sustainable use of marine resources is sought by integrating conservation and economic interests (Douvere, 2008). Within this framework, two important conservation measures are to ensure that new developments such as marine renewables are designed and located to minimize impacts on protected species, and to designate the most important areas for wildlife as Marine Protected Areas (MPAs; Claudet, 2011). For top predators such as seabirds, identifying important areas is challenging because at-sea distribution may vary with environmental conditions (Louzao et al., 2009) and intrinsic mechanisms at the population level (e.g. density dependence, Lewis et al., 2001) or individual level (e.g. sex, Quintana et al., 2011). Furthermore, different components of a population may vary in distribution. For example, individuals from sub-colonies may segregate at sea driven by energetic constraints, competition or use of local information (Hipfner et al., 2007).

An increasingly widespread method of quantifying important areas for seabirds is the deployment of tracking devices on breeding individuals at colonies (Burger and Shaffer, 2008). However, despite the potential for considerable temporal and spatial

* Corresponding author. Tel.: +44 1314454343.
E-mail addresses: marib@ceh.ac.uk (M.I. Bogdanova), swanl@ceh.ac.uk (S. Wanless), frada@ceh.ac.uk (F. Daunt).

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heterogeneity in at-sea distributions, tracking studies of breeding seabirds are often carried out in a small number of years because of challenging timescales to deliver results and in restricted locations within the colony because of logistical constraints. Some of these studies have been strengthened by integrating tracking data with at-sea survey data, and incorporating modeling of habitat association of seabirds to predict distributions (e.g. Louzao et al., 2009). However, the risk is that important foraging areas are being identified based on a narrow set of conditions, potentially jeopardizing their effectiveness in the long term. Furthermore, potential sub-colony effects have largely been ignored yet may be of fundamental importance, since they will determine what proportion of a population is likely to be protected by MPA designation or affected by an anthropogenic development.

To identify important areas for breeding seabirds that consider this spatio-temporal heterogeneity, it is crucial to quantify a population's foraging distribution over a number of years and for different sub-colonies. Furthermore, it is important to determine how environmental conditions or intrinsic mechanisms underpin this variation. Tracking with data loggers is the most appropriate method for assessing distribution of seabirds of known colony origin and breeding status. However, few long-term tracking studies on seabirds exist (Phillips et al., 2008; Weimerskirch et al., 2012; this study). By quantifying among-year and within-population variation in distribution, and the environmental and intrinsic drivers of this variation, such studies can help identify the degree of uncertainty in conclusions drawn from studies where the number of seasons and/or coverage of the colony are limited.

Here, we quantify inter-annual and sub-colony variation in foraging distribution of European shags *Phalacrocorax aristotelis* (hereafter "shags") from the breeding colony on the Isle of May off the coast of south-east Scotland using a tracking data set spanning more than two decades during which environmental conditions, population density and diet composition varied considerably. The species is endemic to the northeast Atlantic. In the UK, it has been in decline for over a decade (JNCC, 2013) and is amber listed as a species of conservation concern (Eaton et al., 2009). As an inshore-feeding, pursuit-diving seabird, the shag may be affected by tidal and wave renewable energy developments (Grecian et al., 2010; Langton et al., 2011). Important areas, including those used for foraging, are potential candidates for designation as Special Protection Areas (SPAs) under the EU Birds Directive (EU, 2009). Therefore, detailed information on foraging distribution is important for the effective identification of protected areas and assessment of potential impacts of human activities. We use our long term tracking data set to: (1) quantify the consistency of important foraging areas across years; (2) assess the minimum number of years of data collection needed to provide a robust estimate of the long-term population foraging distribution; (3) identify extrinsic and intrinsic determinants of foraging range and (4) quantify sub-colony segregation in foraging distributions. We use our results to highlight factors marine spatial planners should consider when making decisions based on less comprehensive data sets.

2. Methods

2.1. Field site and data collection

The study was carried out on the Isle of May National Nature Reserve, south-east Scotland (56°11′N, 2°33′W). Foraging locations of adult shags were obtained using animal-borne instrumentation in 15 breeding seasons over the period 1987–2010. Four methods involving three types of devices were used to estimate foraging location: dead-reckoning from VHF telemetry, triangulation from VHF telemetry, dead reckoning from compass loggers and GPS tracking (Wanless et al., 1991, 2005; see online Appendix A1 for full details). All data were collected during the chick-rearing period except in 2001, when foraging trips during incubation were also recorded. Birds were captured at the nest using a crook, and the tracking device attached to back or central tail feathers using waterproof tape (Tesa Ltd.) and/or cable ties. Birds typically carried devices for short periods (median: 1.2 days; range: 0.6–25 days) before they were recaptured and the device retrieved. No adverse effects were witnessed during capture and handling, and birds returned to the nest within 10 min in all cases where the mate had not assumed nest duties. Device type, sample sizes and deployment period for each year are summarized in Table 1. Birds were sexed by voice and behavior (Snow, 1960).

To explore the effect of density dependence, we used annual breeding population size (number of pairs; Alampo and Ash, 2010), estimated using standardized methods that are employed at seabird monitoring sites in the UK (see Walsh et al., 1995 for data collection protocols). As an integrative measure of environmental conditions (Frederiksen et al., 2007) we used population breeding success, which was the average number of chicks fledged per pair recorded each year in a sample of nests (mean: 142; range: 60–288) using standardized methods (Walsh et al., 1995). The effect of diet composition, as an indicator of availability of different prey, was also explored. Diet composition was determined from food regurgitated by chicks and adults collected opportunistically during fieldwork (samples per year: mean: 37; range: 16–64), from which annual biomass proportions of each diet species was

Table 1
Annual deployment summary over the study period, including original sample size of foraging locations and subsampling of GPS data to enable comparison across years (see main text).

Year	Device type	Deployment period	*n* Birds	*n* Foraging trips	*n* Foraging locations	*n* Subsampled foraging locations
1987	VHF	28 June–24 July	10	NA	139	139
1988	VHF	29 June–17 July	12	NA	85	85
1989	VHF	10 June–5 July	7	NA	106	106
1990	VHF	2 July–8 July	15	23	27	27
1991	VHF	12 July–21 July	24	29	43	43
1992	VHF	1 June–18 July	43	100	159	159
1994	VHF	9 July–22 July	9	41	60	60
1997	VHF	30 May–30 July	41	41	41	41
1998	VHF	22 June–31 July	19	19	19	19
2001	VHF	17 May–7 July	41	48	48	48
2002	Compass	4 June–30 June	16	31	61	61
2003	GPS	1 June–11 June	10	32	1181	50
2008	GPS	19 June–24 June	9	21	1934	42
2009	GPS	3 June–23 June	31	202	8379	469
2010	GPS	8 June–24 June	33	260	7621	463
Total			320	1106	19903	1812