View metadata, citation and similar papers at core.ac.uk

brought to you by CORE

provided by NERC Open Research Archive

Article (refereed) - postprint

Barlow, Emily J.; **Daunt, Francis**; **Wanless, Sarah**; Reid, Jane M.. 2013 Estimating dispersal distributions at multiple scales: within-colony and among-colony dispersal rates, distances and directions in European shags Phalacrocorax aristotelis. *Ibis*, 155 (4). 762-778. 10.1111/ibi.12060

Copyright © 2013 British Ornithologists' Union

This version available http://nora.nerc.ac.uk/506749/

NERC has developed NORA to enable users to access research outputs wholly or partially funded by NERC. Copyright and other rights for material on this site are retained by the rights owners. Users should read the terms and conditions of use of this material at http://nora.nerc.ac.uk/policies.html#access

This document is the author's final manuscript version of the journal article, incorporating any revisions agreed during the peer review process. Some differences between this and the publisher's version remain. You are advised to consult the publisher's version if you wish to cite from this article.

The definitive version is available at http://onlinelibrary.wiley.com

Contact CEH NORA team at
noraceh@ceh.ac.uk

The NERC and CEH trademarks and logos ('the Trademarks') are registered trademarks of NERC in the UK and other countries, and may not be used without the prior written consent of the Trademark owner.

Running headline: Shag dispersal rate, distance & direction

Estimating dispersal distributions at multiple scales: within-colony and among-colony dispersal rates, distances and directions in European shags *Phalacrocorax aristotelis*

EMILY J. BARLOW,[1, 2] FRANCIS DAUNT,[1] SARAH WANLESS[1] & JANE M. REID[2*]

[1]*Centre for Ecology & Hydrology, Bush Estate, Penicuik, EH26 0QB, UK*

[2]*Institute of Biological & Environmental Sciences, School of Biological Sciences, Zoology Building, University of Aberdeen, Tillydrone Avenue, Aberdeen, AB24 2TZ, UK*

[*]Corresponding author

Email: jane.reid@abdn.ac.uk

Knowledge of the rate, distance and direction of dispersal within and among breeding areas is required to understand and predict demographic and genetic connectivity and resulting population and evolutionary dynamics. However dispersal rates, and the full distributions of dispersal distances and directions, are rarely comprehensively estimated across all spatial scales relevant to wild populations. We used resightings of European Shags *Phalacrocorax aristotelis* colour-ringed as chicks on the Isle of May (IoM), UK, to quantify rates, distances and directions of dispersal from natal to subsequent breeding sites both within IoM (within-colony dispersal) and across 27 other breeding colonies covering 1045km of coastline (among-colony dispersal). Additionally, we used non-breeding season surveys covering 895km of coastline to estimate breeding season detection probability and hence potential bias in estimated dispersal parameters. Within IoM, 99.6% of individuals dispersed between their natal and observed breeding nest site. The distribution of within-colony dispersal distances was right-skewed; mean distance was shorter than expected given random settlement within IoM, yet some individuals dispersed long distances within the colony. The distribution of within-colony dispersal directions was non-uniform, but did not differ from expectation given the spatial arrangement of nest sites. However, 10% of all 460 colour-ringed adults that were located breeding had dispersed to a different colony. The maximum observed dispersal distance (170km) was much smaller than the maximum distance surveyed (690km). The distribution of among-colony dispersal distances was again right-skewed. Among-colony dispersal was directional, and differed from random expectation and from the distribution of within-colony dispersal directions. Non-breeding season surveys suggested that the probability of detecting a colour-ringed adult at its breeding location was high at a north-eastern UK scale (98%). Estimated dispersal rates and distributions were therefore robust to incomplete detection. Overall, these data demonstrate skewed and directionally divergent dispersal distributions across small (within-colony) and large (among-colony) scales, and indicate that dispersal may create genetic connectivity but little among-colony demographic connectivity within the study area.

Key-words: connectivity, demography, fat-tailed distribution, long-distance dispersal, movement, philopatry

Dispersal of individuals within and among natal and subsequent breeding areas can create demographic and genetic connectivity among proximate and distant locations, and consequently influence population structure, dynamics and persistence (Hanski 1999, Clobert *et al*. 2001, Nathan *et al*. 2008, Clobert *et al*. 2009). Accurate estimates of dispersal rates within and among breeding areas, and the overall distributions of dispersal distances and directions, are therefore required to understand observed population ecology and predict future change (Rodenhouse *et al.* 1997, Broquet & Petit 2009, Clobert *et al*. 2009). Such estimates, and understanding of underlying processes, are also required to parameterise theoretical models that examine general ecological and evolutionary consequences of dispersal (Chambers 1995, Kot *et al.* 1996, Chapman *et al.* 2007, Nathan *et al*. 2008, Petrovskii & Morozov 2009). However, it is extremely challenging to accurately estimate overall dispersal rates, distances and directions in wild populations, particularly for species that can potentially disperse substantial distances (Koenig *et al*. 1996). The number of systems for which comprehensive dispersal data exist is consequently limited (Clobert *et al.* 2001, Nathan *et al*. 2003, Doligez & Pärt 2008).

One common limitation is that many field studies measure dispersal within restricted areas that are smaller than the distance over which individuals can potentially move (Koenig *et al*. 1996, Cooper *et al.* 2008, Doligez & Pärt 2008). Such studies can be valuable in quantifying small-scale or local movements, and hence in dissecting local population structure and regulation and underlying behavioural processes (Rodenhouse *et al.* 1997, Nathan *et al*. 2003, Tavecchia *et al*. 2008, Sonsthagen *et al*. 2010). However, conclusions may not be valid when extrapolated across larger spatial scales (Hawkes 2009). In particular, systematic observation bias stemming from restricted study areas may cause long-distance dispersal and hence overall dispersal rates and distances to be substantially underestimated (Baker *et al.* 1995, Koenig *et al*. 1996, Nathan *et al.* 2003, Cooper *et al*. 2008). Some studies attempt to correct for such spatial bias in detection rates by estimating the probability that a dispersed individual will be observed as the proportion of available area that was surveyed at successive distances from the point of initial observation (Baker *et al*. 1995, Koenig *et al*. 1996, Winkler *et al*. 2005, Doligez & Pärt 2008, Sharp *et al*. 2008). However, this method assumes that detection probability per unit search area does not vary with distance, which may not be valid (Cooper *et al*. 2008). Furthermore, directional dispersal could substantially affect population structure and dynamics, and information on direction as well as distance is required to describe overall spatial patterns of dispersal and linkage. Despite this, few field studies have quantified the

full distribution of dispersal directions or tested whether this distribution departs from random expectation given the spatial distribution of available habitat (e.g. Coulson & Néve de Mévergnies 1992, Matthysen *et al*. 2005, Sharp *et al.* 2008). Such estimates may also be biased by arbitrary study area dimensions.

These difficulties, which result from spatially restricted observation effort and hence spatially biased detection rates, are widely accepted to affect many empirical estimates of dispersal rates, distances and directions (Koenig *et al.* 1996, Winkler *et al*. 2005, Cooper *et al*. 2008, Doligez & Pärt 2008). However accurate estimates are required to design and parameterise predictive models that involve dispersal processes (Kot *et al.* 1996, Hanski 1999, McCallum 2000, Petrovskii & Morozov 2009). Two continuous probability distributions, Gaussian (normal) and negative exponential, are often used to approximate the decline in frequency of individuals with increasing distance from a source (Chambers 1995, Kot *et al*. 1996, McCallum 2000, Nathan *et al*. 2003, Chapman *et al*. 2007). Available empirical data, however, suggest that true distributions of dispersal distances can show lower rates of decay at large distances than expected under these models, resulting in 'fat-tailed' distributions (Kot *et al*. 1996, Nathan *et al*. 2003, Chapman *et al*. 2007, Kesler *et al.* 2010). This lack of congruence between basic model formulation and true dispersal distribution may cause divergence between predicted and observed consequences for population structure and evolutionary dynamics (Kot *et al*. 1996, Chapman *et al*. 2007). Individuals that lie within the tails of such distributions are by definition uncommon, and few empirical studies cover sufficiently large areas relative to a species' typical dispersal distance with sufficiently high detection probability to quantify the rate, distance and direction of long-distance dispersal (Nathan *et al*. 2003, 2008). Full natal dispersal distributions have been most comprehensively quantified in passive dispersers (Nathan *et al*. 2008), and in active dispersers that move over relatively small areas or distances (e.g. ≤1km, Stream Salamander *Gyrinophilus porphyriticus*, Lowe 2010; <2km^2, Tansy Beetle *Chrysolina graminis*, Chapman *et al*. 2007). Kesler *et al*. (2010) estimated Red-cockaded Woodpecker *Picoides borealis* dispersal distances within a *c*.1000km^2 area, but this may still be small relative to the species' potential mobility. The frequency and magnitude of long-distance dispersal, and hence the degree to which common model formulations may generally capture the full distributions of dispersal distances and directions across diverse taxa, therefore remain unclear (Nathan *et al*. 2003, 2008, Chapman *et al*. 2007).

To determine the degree to which distributions of local dispersal distances and directions relate to distributions that encompass the full dispersal range, both local and large-scale dispersal need to be measured and then combined to generate overall distributions that incorporate movement across both spatial scales (Hawkes 2009). This requires studies that quantify dispersal rates, distances and directions by locating philopatric and dispersed individuals across the full range of potential dispersal distances and directions within and beyond specific breeding areas, where sampling and hence detection rates are high and relatively uniform across the full range of spatial variation, and where the magnitude and pattern of detection failure and resulting bias can be independently estimated (Baker *et al*. 1995, Koenig *et al*. 1996, Nathan *et al*. 2003, Cooper *et al*. 2008, Doligez & Pärt 2008).

We used individually marked European Shags *Phalacrocorax aristotelis* to quantify the rate of dispersal from natal to subsequent breeding sites, and the distributions of dispersal distances and directions, both within a focal breeding colony and across the full biologically likely dispersal range from this colony. Furthermore, by locating marked individuals in non-breeding (wintering) areas, we estimated the probability of detecting an individual at its breeding location across a large geographical range and hence the degree of detection failure. We thereby quantified small- and large-scale dispersal distributions, and compared observed distributions to widely implemented model formulations.

METHODS

Study system

The European Shag (hereafter Shag) is a colonially breeding seabird that is endemic to rocky coasts of the north-east Atlantic and Mediterranean (Wanless & Harris 2004). British Shags of all ages are coastally distributed year-round (Harris & Swann 2002). They first breed aged ≥2 years (Potts *et al*. 1980) and adults can be reliably distinguished from subadults by plumage and behaviour (Snow 1960).

Shag demography has been studied for >30 years at a breeding colony on the Isle of May (hereafter IoM; *c.*4km in circumference, 56°11'N 2°33'W), Firth of Forth, eastern Scotland, (Aebischer 1995). Shag chicks have been ringed in all parts of the colony since 1997 with alphanumeric British Trust for Ornithology (BTO) rings and plastic colour-rings engraved with a unique three letter code. A mean of 650 chicks (±365SD, range=161-1208) was ringed

each year during 1997-2006, totalling 6496 individuals and comprising *c*.90% of individuals fledged on IoM during this time. Colour-ring codes can be read in the field at distances of ≤150m, allowing individual Shags to be identified on breeding and wintering grounds without recapture. The annual survival probability of breeding adults is 0.86±0.03SE (Frederiksen *et al*. 2008) meaning that adults commonly survive to breed in multiple years.

Within-colony dispersal

Shags nest on coastal rock ledges on IoM (Aebischer *et al*. 1995). Nest sites are discrete and patchily distributed around the island's circumference. All nest sites are individually marked and their locations are recorded to the nearest 10m using GPS. All nest sites were repeatedly checked during the 2008 and 2009 breeding seasons (1 March-31 August) and the identities of ringed breeding adults were recorded. Sexes were determined by voice, size and behaviour (Snow 1960).

Dispersal within IoM was defined as the movement of an individual from its natal nest site (in 1997-2006) to its observed breeding site in 2008 or 2009. Exact natal sites and hence locations were known for a substantial proportion of colour-ringed adults found breeding on IoM during 2008-2009 (69%, see Results). Dispersal rate was estimated as the number of adult Shags colour-ringed as chicks on IoM found breeding at an IoM site other than their natal site to the total number of these adults found breeding anywhere on IoM. Dispersal distance for these individuals was estimated as the shortest distance around the IoM coastline (coastal distance). Since Shags rarely cross land in flight (Harris & Swann 2002), this was deemed more biologically relevant than Euclidean distance. In practice, coastal and Euclidean distances were tightly correlated (r=0.83, d.f.=284, P<0.0001). Dispersal direction was calculated as the direct bearing from an individual's natal site to its observed breeding site. Since IoM has a roughly elliptical coastline within-colony dispersal in almost any direction was possible, and multiple directions were possible for most distances. Breeding adults that originated from natal sites that were less precisely known, typically due to less comprehensive documentation during early study years, were excluded from these analyses.

Our working definition of dispersal (above) does not equate to natal dispersal defined as movement from natal site to site of first reproduction (Greenwood & Harvey 1982). Our dataset comprised breeding adults of various ages and therefore measured natal dispersal plus any subsequent breeding dispersal between breeding sites. Ultimately, it is the combination of

these two processes, as described by our study, that influences demographic and genetic connectivity and hence population and evolutionary dynamics. Phenomenological understanding of these consequences therefore does not necessarily require the two dispersal processes to be distinguished. However, to investigate the degree to which breeding dispersal might bias inference of natal dispersal *sensu stricto* from our data, coastal distance was calculated between the 2008 and 2009 breeding sites of adults (aged 2-12 years) that had been ringed as chicks on IoM that bred in both years (n=276). These data showed that breeding dispersal was highly restricted in both males and females (mean 15m±66SD, median 0m, IQR 0-8m). Indeed, 140 (51%) of the 276 adults bred at the same site in both years, and 265 (96%) bred within 50m of their previous site. Breeding dispersal distances did not differ significantly between males and females (Kolmogorov-Smirnov: D=0.05, P=0.99) or between 2008 and 2009 breeding sites relative to an individual's natal site (Kolmogorov-Smirnov: D=0.04, P=0.99). Furthermore, 70% of adults that changed breeding site between 2008 and 2009 moved <5° between these sites relative to their natal site. Breeding dispersal directions did not differ significantly between sexes (Kolmogorov-Smirnov: D=0.08, P=0.36) or between 2008 and 2009 breeding sites relative to an individual's natal site (Kolmogorov-Smirnov: D=0.06, P=0.99). Previous analyses also showed that breeding dispersal is restricted in Shags (Aebischer *et al*. 1995). These data suggest that breeding dispersal would not greatly bias inference of natal dispersal distributions from our composite dispersal data. Since the nest sites of individuals that bred in both 2008 and 2009 were clearly non-independent (being identical in 51% of cases and <50m apart in most others), a single randomly selected breeding site from 2008 or 2009 was used to estimate dispersal distance and direction from natal to subsequent breeding location for individuals that bred in both years.

Among-colony dispersal

Dispersal away from IoM was defined as the movement of an individual that had been ringed as a chick on IoM to an observed breeding location elsewhere. To locate dispersed adults, 26 colonies in addition to IoM were surveyed during the 2008 and/or 2009 breeding seasons, and one further colony was surveyed in 2010 (Fig.1a, Table 1). Surveys were carried out by the authors, assisted by other observers (see Acknowledgements). Colonies were identified during a census of all UK Shag populations in 1998-2002 and ranged in size from <10 to >500 breeding pairs at that time (Table 1; Wanless & Harris 2004), and fell within an overall study area that was defined by long-term UK and European ring-recovery data. Specifically,

since 1997, 425 adult Shags ringed as chicks on IoM were recovered elsewhere, dead or alive in any season, prior to the current study. These data do not themselves accurately describe breeding locations or dispersal rates, but do help define the total geographical area relevant to adult IoM Shags. All 425 recoveries occurred along the UK's east (North Sea) coast, ranging from 427km north of IoM (*n*=375) to 355km south (*n*=50). Dead recovery data prior to 1985 showed similar patterns (Galbraith *et al*. 1986). This does not solely reflect the geographical distribution of recovery reporting because numerous Shags ringed at other UK colonies have been recovered elsewhere, including on north, south and west UK coasts and continental Europe (Harris & Swann 2002). This weight of prior information suggests that dispersal of IoM-ringed Shags to geographical regions other than North Sea colonies is unlikely or extremely rare. The 27 surveyed colonies were consequently restricted to the North Sea. However, they still encompassed a large geographical area relative to all previous ring recoveries, from 690km north (16 colonies) to 355km south (11 colonies) of IoM, covering 1045km of coastline in total (Fig.1a). Approximately 90% of all breeding colonies along the UK's North Sea coast were surveyed (as per Wanless & Harris 2004) during the main incubation and chick-rearing periods (i.e. April-July). The remaining 10% comprised small colonies and scattered breeding pairs. No breeding colonies exist between the Farne Islands and Flamborough Head (*c*.100km and *c*.355km south of IoM respectively) or south of Flamborough Head due to a lack of suitable nesting habitat. The most northerly and southerly colonies surveyed therefore represent the approximate limits of breeding colonies along the North Sea coast and encompass the maximum likely dispersal distance of IoM Shags (and substantially exceeded the maximum distance observed, see Results).

At each surveyed colony as many adult Shags as possible were checked for colour-rings by observation from land and/or boat. All adult Shags observed at a colony during the breeding season were assumed to be breeding at that colony. No adults were observed at multiple colonies within or between 2008 and 2009. There was therefore no evidence of among-colony breeding dispersal. Not all adults observed during any one survey could be checked for rings because their legs were obscured from view. These individuals were counted and categorised as 'unchecked'. Checked adults were counted and categorised as 'unringed' or 'colour-ringed'. Ring codes were recorded and verified by repeat checking by the observer, between observers or using digital photography. It was highly unlikely that all Shags breeding at a particular colony would be present during a single survey and/or checked if present. Therefore, to increase the probability that colour-ringed individuals would be

observed, multiple surveys of each colony were undertaken where possible. The total number of individuals checked for colour-rings across all visits to each colony was estimated (Supporting Information Appendix S1). To investigate whether the distribution of colour-ringed adults found breeding simply reflected the distribution of observation effort we quantified the correlation between the number of ringed adults observed and the total number of adults estimated to have been checked across all surveyed colonies. Sex could not be reliably determined for most adults observed away from IoM due to generally greater observation distances and reduced opportunity for prolonged behavioural observations.

The observed dispersal rate away from IoM was estimated as the ratio of the number of adult Shags that had been colour-ringed as chicks on IoM that were found at breeding colonies away from IoM to the total number of these adults found at all colonies including IoM. The distribution of dispersal distances was quantified using coastal distance between IoM and the other 27 surveyed colonies. Coastal distance was calculated as above or as the shortest distance across the water for distances ≤50km (since shags can cross such distances of open sea, Harris & Swann 2002). Coastal distance was again tightly correlated with Euclidean distance (Spearman's rank correlation coefficient: r=0.99, P<0.0001). Dispersal directions were calculated as the bearing from IoM to each surveyed colony.

Overall dispersal

Data from all surveys within and outside IoM were combined to quantify the overall distribution of dispersal distances and directions across the full range of individual dispersal.

Analyses

Individual-based randomisations were used to test whether observed distributions of dispersal distances and directions differed from random expectation given the system's spatial properties. For all adults observed breeding on IoM during 2008-2009 with known natal nest sites, randomised dispersal distributions were generated by calculating distance and direction between each adult's natal site and a breeding site that was randomly selected with replacement from all nest sites used on IoM during 1997-2009 (n=2024). This process was repeated 1000 times for each adult. Data were binned into 40x50m distance categories (0-2000m), which were deemed biologically relevant based upon observed dispersal distances, and averaged across randomisations for each distance category to produce the mean (±SD) randomised distance distribution. The same method was used to produce a randomised

direction distribution, with data binned into 18x20° categories (0-360 degrees). Observed distances and directions were binned into the same categories for comparison.

Similar methods were used to create randomised null distributions for dispersal among colonies and overall. For colour-ringed adults observed breeding away from IoM during 2008-2010, random breeding colonies were selected with replacement from all surveyed colonies. In the absence of accurate data quantifying site availability at surveyed colonies, settlement probability was weighted by approximate colony size with settlement being three times more likely at large colonies than small colonies (Table 1). Conclusions remained robust when these weightings were altered, including equal weighting. Randomised dispersal distances and directions were calculated and categorised by colony (n=27). Randomised distributions for overall dispersal were generated by calculating distance and direction between an individual's known natal site and a random breeding colony (including IoM) selected with replacement. Individuals that were randomly allocated to IoM were assigned a random breeding site within IoM. Distances were categorised by colony (n=28) and directions were binned as before. Finally, to investigate whether observed dispersal directions differed from expectation given constrained dispersal distances, randomisations were repeated with destination colonies restricted to surveyed colonies located within the maximum observed dispersal distance.

Since Shags occupy discrete breeding colonies, dispersal occurs in discontinuous rather than continuous space. However, to quantify the degree to which the observed dispersal distribution could be adequately captured by commonly used dispersal models, observed distance distributions were tested against negative exponential and Gaussian distributions (the latter reflected and centred on zero, Kot *et al*. 1996). Skew and kurtosis were calculated for unreflected observed distance distributions (Joanes & Gill 1998; Chapman *et al*. 2007). Values of >1 indicate distributions that are right-skewed and fatter-tailed than expected under normality. Observed direction distributions were tested against a Rayleigh (circular) distribution to determine whether they differed from uniformity. Circular-linear regressions were used to quantify the relationship between dispersal distance (linear variable) and direction (circular variable) and test whether distance was non-random with respect to direction.

Detection rate

Despite our substantial large-scale survey effort, as with any field dispersal study, the probability of detecting a colour-ringed breeding Shag was unlikely to be 1.0 and may have varied among colonies (Supporting Information Appendix S2). To assess the degree to which incomplete and uneven detection of breeding adults might bias estimated dispersal rates, distances or directions, the number of colour-ringed adults that were alive but had not been located at any breeding colony was estimated by undertaking winter (1 September-28 February) surveys during the 2008-2009 and 2009-2010 winters. During winter, Shags congregate at roosts on skerries and piers that often include large numbers of individuals fledged from and breeding at multiple colonies; individuals can winter substantial distances (>150km) from their breeding colony (Supporting Information Appendix S3). The probability of observing an individual in winter is therefore at least partly independent of its breeding location. Any spatial bias in detection probability with respect to breeding location therefore differs to some degree between summer and winter. Twenty winter roosts were surveyed, ranging from 540km north to 355km south of IoM (Fig.1b, Supporting Information Appendix S3). All observed Shags were checked for colour-rings and identities of ringed adults were verified using similar protocols as at breeding colonies.

The number of colour-ringed adults that were observed during winter surveys but not observed breeding (N_U) was used to estimate the total number of colour-ringed adults that were alive but had not been located breeding (N_X), as:

$$N_X = N_U/(N_{WTOT}/N_{STOT}) \quad \text{eqn.1}$$

where N_{WTOT} is the total number of colour-ringed adults observed during winter surveys that had also been located breeding, and N_{STOT} is the total number of colour-ringed adults observed breeding across all surveyed colonies (Supporting Information Appendix S2). This expression assumes that the probability that an individual will be observed in winter is independent of the probability that it was observed breeding in the summer. It therefore provides an approximate estimate of the total number of individuals that remained undetected during breeding season surveys. The N_X breeding adults that were estimated to have remained undetected was used to estimate upper and lower limits to dispersal rate away from IoM, as:

322 Upper limit = $(N_{SD}+N_X)/(N_{SD}+N_{SIoM}+N_X)$ eqn.2a

323 Lower limit = $N_{SD}/(N_{SD}+N_{SIoM}+N_X)$ eqn.2b

324 where N_{SD} is the total number of colour-ringed Shags observed breeding away from IoM
325 during 2008-2010 and N_{SIoM} is the total number of colour-ringed Shags observed breeding on
326 IoM during 2008-2009.

327 To estimate the degree to which incomplete detection of breeding adults might have caused
328 observed dispersal distributions to be poorly estimated, the estimated N_X undetected adults
329 were either allocated to IoM, or randomly allocated to one of the 27 other surveyed colonies,
330 with a probability weighted by colony size (Table 1). Randomisations were repeated 1000
331 times, summarised as before and compared to observed distances and directions. Upper and
332 lower limits to dispersal rate and distributions respectively assume that all N_X undetected
333 colour-ringed adults had dispersed from IoM, or that all bred on IoM (Supporting Information
334 Appendix S2).

335 Data from all surveys undertaken during 2008-2010 were combined for all analyses.
336 Analyses were run in Excel and R (v.2.12.2, R Development Core Team 2011). Circular
337 statistics were calculated using library 'circular' (Lund & Agostinelli 2011). Means are
338 presented ±1SD.

339 **RESULTS**

340 **Within-colony dispersal**

341 During the 2008 and 2009 breeding seasons 1511 observations were made of 938 individual
342 adult Shags breeding on IoM (Table 1). In total, 416 adult Shags that had been ringed as
343 chicks on IoM were located breeding on IoM. Exact natal nest sites were known for 285 of
344 these 416 individuals (69%). Only one individual (0.3%) bred at its natal site. The observed
345 dispersal rate within IoM was therefore 99.6%. This rate did not differ significantly from that
346 expected given random dispersal to any possible nest site (χ^2=1.77, d.f.=1, *P*=0.18);
347 recruitment to the natal site occurred on 0.03% of random allocations.

Observed dispersal distances within IoM ranged from 0 to 1962m (mean 464±500m, median 249m, IQR 65-799m, n=285). Distributions did not differ significantly between males and females (Kolmogorov-Smirnov: D=0.25, P=0.16; Fig.2a). Across both sexes, the distribution of dispersal distances differed significantly from both negative exponential and Gaussian (Kolmogorov-Smirnov: D=0.13, P<0.0001 and D=0.48, P<0.0001 respectively), and was right-skewed and fat-tailed (skew=3.6, kurtosis=14.2). Randomised dispersal distances ranged from 0 to 2048m (mean 756±512m, median 733m, IQR 276-1153m). Observed dispersal distances tended to differ from random for females (χ^2=56, d.f.=39, P=0.06; Fig.2c), and differed significantly from random for males (χ^2=77, d.f.=39, P=0.006; Fig.2b) and across both sexes combined (χ^2=85, d.f.=39, P<0.01); individuals bred closer to their natal site than expected given random dispersal within IoM.

Some dispersal occurred in almost every direction within IoM (Fig.3a). However the observed distribution of dispersal directions was bimodal and differed markedly from uniformity (Rayleigh test: z=0.18, n=285, P<0.0001; Figs. 3a, 4a); 18% (51/285) of individuals dispersed approximately SE (112.5-157.5°) from their natal site and 34% (97/285) of individuals dispersed approximately NW (292.5-337.5°; Fig.3a). Observed dispersal directions did not differ significantly between males and females (Kolmogorov-Smirnov: D=0.13, P=0.22; Fig.3a). Randomised dispersal directions were also bimodal: 23% and 36% of directions were approximately SE and NW respectively. This bimodal distribution arises because the IoM is roughly elliptical and aligned approximately SE-NW. The observed and randomised distributions of dispersal directions did not differ significantly for either males (χ^2=10.9, d.f.=17, P=0.98; Fig.3b) or females (χ^2=5.3, d.f.=17, P=0.99; Fig.3c) or across both sexes combined (χ^2=11.3, d.f.=17, P=0.98). The observed directionality of dispersal therefore did not differ from that expected given random movement among nest sites. Dispersal distance was not strongly related to dispersal direction (circular-linear regression: estimate=-0.08 radians/m, t=0.50, P=0.31, n=285).

Among-colony dispersal

During the 2008 to 2010 breeding seasons, 99 surveys at 27 colonies away from IoM resulted in 7648 observations of an estimated c.3487 individual adult Shags (Table 1, Fig.5, Supporting Information Appendix S1). A total of 44 colour-ringed adults that had been ringed as chicks on IoM were located breeding at these colonies. The observed dispersal rate away from IoM was therefore 44/(416+44)=9.6%. The number of colour-ringed adults found

breeding at a colony was not tightly correlated with the total number of adults estimated to have been checked there across all surveys (r =0.18, d.f.=26, P=0.35; Fig.5, Supporting Information Appendix S1).

At least one colour-ringed adult was located at 12 of 27 surveyed colonies (Table 1, Fig.5). Observed dispersal distances ranged from 16 to 170km (mean 62±46km, median 40km, IQR 35-99km, n=44). The observed distance distribution tended to fit negative exponential but differed significantly from Gaussian (Kolmogorov-Smirnov: D=0.23, P=0.015 and D=0.5, P<0.0001 respectively). The distribution was right-skewed and fat-tailed (skew=2.3, kurtosis=3.9); 64% (28/44) of dispersed Shags were located at colonies within 50km of IoM. Randomised dispersal distances ranged from 13 to 689km (mean 170±4km, median 100km, IQR 50-229km). Observed distances differed significantly from random (χ^2=39, d.f.=26, P=0.04); most individuals dispersed to colonies that were closer to IoM than expected given random dispersal across surveyed colonies. However, dispersers did not all move to the closest colonies to IoM (Table 1).

The observed distribution of dispersal directions differed from uniformity (Rayleigh test: z=0.42, n=44, P<0.0001; Fig.4b). Most individuals dispersed SW from IoM; 64% (28/44) moved between 202.5 and 247.5° (Fig.4b). Furthermore, the observed distribution differed from that expected given random settlement across all surveyed colonies (χ^2=38, d.f.=26, P=0.05) and across only those colonies up to the maximum observed dispersal distance (χ^2=35, d.f.=17, P=0.005). This indicates that the observed directionality of dispersal did not solely reflect the spatial distribution of surveyed colonies. Observed dispersal directions varied significantly with dispersal distances (circular-linear regression: estimate=0.015 radians/km, t=5.33, P<0.0001, n=44); Shags moved furthest towards the NE. However, randomised distances and directions were also significantly related (circular-linear regression: estimate=0.017 radians/km, t=2.52, P=0.005) indicating that this distance-direction relationship simply reflects the system's spatial structure.

Overall dispersal

Since the distributions of dispersal distances and directions within IoM did not differ between males and females and most Shags observed away from IoM could not be reliably sexed, the dispersal distributions for Shags observed within (n=285) and away from IoM (n=44) were combined (n=329).

411 The full observed distribution of dispersal distances ranged from 0-170km (mean 9±27km,
412 median 0.32km, IQR 0.08-1km, *n*=329; Fig.6). It differed significantly from both negative
413 exponential and Gaussian (Kolmogorov-Smirnov: *D*=0.85, *P*<0.0001 and *D*=0.13, *P*<0.0001
414 respectively) and was right-skewed and fat-tailed (skew=4.8, kurtosis=20.0). Randomised
415 dispersal distances ranged from 0 to 689km (mean 3±26km, median 0.64km, IQR 0.27-
416 1.05km) and differed significantly from observed (χ^2=478, d.f.=27, *P*<0.0001) demonstrating
417 highly significant philopatry to and within the IoM colony.

418 The full observed distribution of dispersal directions was bimodal; 17% (56/329) of Shags
419 dispersed approximately SE and 30% (98/329) dispersed approximately NW (Fig.4c). This
420 distribution differed significantly from that expected given random dispersal to any nest site
421 or surveyed colony (χ^2=230, d.f.=17, *P*<0.0001), and to any nest site or surveyed colony
422 within the observed dispersal range (χ^2=45, d.f.=17, *P*=0.002). The overall distribution of
423 dispersal directions did not, therefore, simply reflect the system's spatial structure. Neither
424 observed distances (circular-linear regression: estimate=0.49 radians/km, *t*=0.89, *P*=0.18) nor
425 randomised distances (circular-linear regression: estimate=1.34 radians/km, *t*=0.46, *P*=0.33)
426 were significantly related to dispersal direction.

427 **Detection rate**

428 A total of 195 adults that had been ringed as chicks on IoM were resighted at roosts during
429 the winters of 2008-2009 or 2009-2010, and were observed up to 430km from their known
430 breeding colony (Supporting Information Appendix S3). These included 178 (43%) of 416
431 individuals observed breeding on IoM, and 13 (30%) of 44 individuals observed breeding at a
432 different colony. These proportions did not differ significantly (χ^2=0.96, d.f.=1, *P*=0.33). The
433 remaining four individuals were not observed breeding at any colony, giving N_U=4. The total
434 number of undetected breeding-age adults was therefore estimated to be small (N_X≈9, eqn.1).
435 The lower and upper limits to the rate of dispersal away from IoM were therefore estimated
436 as *c*.9% and 11% respectively (eqns.2a & b).

437 The overall observed distributions of dispersal distances and directions did not differ
438 significantly from those created when N_X=9 undetected adults were randomly allocated to
439 nest sites on IoM (distance: χ^2=0.02, d.f.=27, *P*=0.99, direction: χ^2 =2.19, d.f.=17, *P*=0.97), or
440 to surveyed breeding colonies away from IoM (distance: χ^2=3.89, d.f.=27, *P*=0.99; direction:
441 χ^2=0.39, d.f.=17, *P*=0.99; Supporting Information Appendix S2). Estimated dispersal rates

and distributions were therefore broadly robust to the small estimated degree of incomplete detection in our study, and hence to the maximum potential degree of spatial bias in detection.

DISCUSSION

Understanding the ultimate consequences of dispersal for population structure and dynamics requires accurate estimation of the rate, distance and direction of movements between natal and subsequent breeding locations, both within single breeding areas and across a population or species' full potential dispersal range (Rodenhouse *et al*. 1997, Frederiksen & Petersen 1999, Broquet & Petit 2009, Clobert *et al*. 2009). We estimated within-colony, among-colony and overall dispersal rates, distances and directions for Shags, a species with substantial dispersal potential, by locating adults that had been colour-ringed as chicks on the Isle of May (IoM) breeding on IoM and at other colonies across a large geographical scale. We additionally used winter surveys to estimate the degree of incomplete detection of breeding adults, and hence consider resulting error and bias in estimated dispersal distributions.

Within-colony dispersal

The Isle of May is a discrete island land mass. Its Shag population is monitored annually; most fledglings are ringed and adults identified with little internal spatial bias. The within-colony dispersal rate and full distributions of dispersal distances and directions were therefore estimated with little potential bias stemming from arbitrary boundaries or spatially heterogeneous sampling. The internal dispersal rate, defined as observed breeding away from an individual's natal nest site, was close to 100%. This did not differ from expectation assuming unconstrained dispersal among all known nest sites. The high internal dispersal rate may therefore simply reflect high nest availability rather than necessarily implying specific avoidance of, or constraints on, occupying the natal site. Equally, there was no evidence that Shags bred on their natal site more than expected by chance.

However, despite the high internal dispersal rate, dispersal distances within IoM were shorter than expected given random dispersal in males and females (medians of 205m and 258m versus 736m and 730m respectively; Fig.2). Dispersal was therefore restricted at a biologically small spatial scale. Since Shags can forage up to 15km away from their nest while breeding (Wanless *et al.* 1991) and move up to *c*.400km during winter (Supporting

Information Appendix S3) this relative philopatry cannot reflect a physical inability to disperse throughout the colony; the entire circumference of IoM is only 4km. Several other studies have demonstrated restricted within-colony dispersal for highly vagile species (e.g. Black-legged Kittiwakes *Rissa tridactyla*, Coulson & Néve de Mévergnies 1992; Western Gulls *Larus occidenalis*, Spear *et al.* 1998; Black Guillemots, *Cepphus grylle*, Frederiksen & Petersen 1999; Wandering Albatross *Diomedea exulans*, Charmantier *et al*. 2011). Such strong natal philopatry can lead to genetic structuring and demographic asynchrony at small spatial scales (e.g. Tavecchia *et al.* 2008, Sonsthagen *et al*. 2010). However, despite their overall tendency to breed relatively near their natal site, a substantial proportion of Shags dispersed greater distances within IoM (e.g. 48/285 dispersed ≥1km, including both males and females; Fig.2). Any within-colony genetic structure is therefore likely to be eroded by gene flow (Mills & Allendorf 1996).

Directional dispersal could substantially alter population processes beyond those resulting from specific dispersal rates and distances (Kot *et al*. 1996, Clobert *et al*. 2001, Matthysen *et al*. 2005, Sharp *et al*. 2008). An individual's dispersal direction is inevitably constrained by the location of its natal site relative to other potential breeding sites. Since IoM has a roughly elliptical coastline, individual Shags could potentially disperse in multiple directions from any natal site. Furthermore, across the whole colony combined, some individuals had opportunity to disperse in every direction. In fact, the observed distribution of dispersal directions was bimodal rather than uniform, but did not differ from that expected given random dispersal among nest sites. The observed directionality of dispersal can therefore be explained by local landscape structure rather than necessarily implying preferential directional movement by individual Shags.

Dispersal distances and directions within IoM were very similar in males and females. This contrasts with the general observation that females often disperse longer distances in birds (Greenwood 1980), but is consistent with studies on Western Gulls (Spear *et al.* 1998) and Lesser Kestrels (*Falco naumanni*, Serrano *et al*. 2003). A previous study on IoM Shags did detect non-significant female-biased dispersal over a larger spatial scale (Aebischer 1995). However, this study took place when the IoM population was much larger than it was in 2008-2009, and followed a period of rapid increase. This indicates that general conclusions regarding sex-biased dispersal cannot necessarily be drawn from single studies that are restricted in time or space (Lawson-Handley & Perrin 2007).

Among-colony dispersal

The rate and pattern of long-distance dispersal could profoundly affect population and evolutionary dynamics. One basic aim in ecology is therefore to accurately quantify dispersal rates, distances and directions among breeding areas on a large spatial scale. Such data are challenging to collect because long-distance dispersal may be rare and search areas may be large (Baker *et al*. 1995, Koenig *et al*. 1996, Nathan *et al*. 2003, Cooper *et al*. 2008). Estimated dispersal rates, distances and directions will be prone to error and bias if some individuals remain undetected and these individuals are non-random with respect to breeding location (Baker *et al*. 1995, Koenig *et al*. 1996). We minimised these ubiquitous problems by surveying most Shag breeding colonies across a substantial area relative to the total likely dispersal range from IoM (Table 1, Fig.1). Since colonies are restricted to coastline and islands, the search area did not increase non-linearly with distance from IoM (as would occur in a fully two-dimensional landscape, Lowe 2010). Overall, approximately 28% (2126/7648; Table 1) of all observations of breeding Shags and 32% (1107/3487; Table 1) of the estimated total number of individuals checked away from IoM were further away from IoM than the furthest observed disperser. Therefore, while the occurrence of rare long-distance dispersal over even greater distances than those surveyed cannot be rules out, our search area substantially exceeded the likely and detected dispersal range. The number of dispersers located at each colony away from IoM was not correlated with the number of individuals estimated to have been checked there (Table 1, Supporting Information Appendix S1) suggesting that observed disperser locations did not solely reflect the distribution of observation effort across surveyed colonies. Furthermore, our surveys of marked adults both at breeding colonies and on separate wintering grounds enabled us to estimate breeding season detection failure with relatively independent spatial bias. The use of independent cross-season observations to validate dispersal estimates has been proposed but rarely implemented (Doligez & Pärt 2008). Our winter observations indicated that the probability of detecting a IoM-ringed Shag at its future breeding location was very high (460/469=98%) at a north-east UK scale. The estimated number of undetected breeders was therefore too few to substantially alter the main conclusions regarding the distributions of dispersal distances and directions, and indicated that the observed dispersal rate of *c.*10% was robust to ±1% (see also Supporting Information Appendix S2). Although the estimated breeding season detection failure was small in the current study, our use of cross-season observations illustrates one means by which the long-standing problem of how to quantify overall detection failure in large-scale dispersal studies could be resolved (Doligez & Pärt 2008).

538 Observed dispersers moved to colonies that were much closer to IoM than expected if
539 dispersal occurred at random across all surveyed colonies, demonstrating that dispersal was
540 spatially restricted among colonies as well as within the focal IoM colony (and hence at two
541 very different spatial scales). Most dispersing Shags moved SW from IoM, but the longest
542 movements were to the NE. This broad relationship between distance and direction mirrored
543 the geographical distribution of surveyed colonies. These patterns imply that it may be
544 distance rather than direction *per se* that shapes the overall dispersal distribution. However
545 the distribution of among-colony dispersal directions did differ from random expectation,
546 even after accounting for distance. This indicates that among-colony dispersal does have a
547 non-random directional component in Shags.

548 Shag dispersal away from IoM (*c*.10%) occurred at a relatively low rate compared to avian
549 dispersal studies that attempted to correct for bias stemming from restricted study areas (e.g.
550 83% in Lesser Kestrels *Falco naumanni*, Serrano *et al*. 2003 and 80% in Tree Swallows
551 *Tachycineta bicolor*, Winkler *et al*. 2005). In other seabirds, natal colony return rates have
552 been estimated to vary widely, from *ca*.10% in Northern Fulmars (*Fulmarus glacialis*,
553 Ollason & Dunnet 1983) to *ca*.80% in Wandering Albatrosses (Inchausti & Weimerskirch
554 2002). The number of observed dispersed Shags never exceeded c.9% of the total adults
555 estimated to have been checked at any colony, and was typically substantially less than this
556 (Table 1). Dispersal from IoM to any other individual colony may consequently be
557 proportionally too infrequent to cause substantial demographic coupling. However, since just
558 one disperser per generation can be sufficient to homogenise genetic variation across
559 populations (Mills & Allendorf 1996), such movements may be sufficient to erode genetic
560 structure.

561 **Overall dispersal**

562 Ecological and evolutionary models of movement commonly assume either Gaussian or
563 negative exponential dispersal functions (Chambers 1995, Kot *et al.* 1996, McCallum 2000,
564 Chapman *et al*. 2007). These functions fitted our data relatively poorly since they failed to
565 account for long-distance dispersal; 'fat-tailed' distributions of dispersal distances were
566 observed at within-colony and among-colony scales and overall. Since Shags are restricted to
567 coastal breeding colonies they do not occupy continuous space. Indeed, distributions of
568 dispersal directions were non-uniform across both spatial scales, violating another standard
569 assumption of phenomenological dispersal models.

These results concur with the growing evidence that dispersal typically does not represent a single process across multiple spatial scales (e.g. Kot *et al*. 1996, Ronce 2007, Petrovskii & Morozov 2009, Kesler *et al*. 2010). Distances and directions were constrained differently by the geography and dimensions of habitat across scales. Within-colony dispersal data therefore did not accurately predict dispersal distributions across larger spatial scales, demonstrating the need to quantify movements across the full extent of dispersal, rather than extrapolating from finite or arbitrary study sites (Nathan *et al*. 2003, Hawkes 2009).

Genetic and demographic connectivity ultimately stem from the spatial distributions of all breeding attempts made by individuals from specific origins (as we measured for Shags originating on IoM). However, full comprehension of the ecological and evolutionary causes of dispersal may require mechanistic as well as phenomenological understanding of observed dispersal distributions (Nathan *et al*. 2008, Clobert *et al*. 2009, Hawkes 2009). Considering stepwise movements between natal and breeding colonies may not be appropriate in Shags, because the range of individual winter movements covers numerous potential breeding colonies (Supporting Information Appendix S3). Observed dispersal may therefore reflect departure and settlement decisions rather than constraints on transience (Hénaux *et al.* 2007; Clobert *et al.* 2009, Hawkes 2009), which may in turn reflect local ecology. Current dispersal away from IoM is unlikely to be driven by local nest site or food availability. The current IoM population is small compared to the recent maximum (1916 pairs in 1987 versus 465 in 2009; Aebischer & Wanless 1992) and breeding success is relatively high (1.90-2.02 chicks fledged per pair in 2008-2009 compared to the mean for 2000-2009 of 1.35 and the long-term mean of 1.01; Newell *et al*. 2010). A key next step is to link quantitative data on dispersal distances and directions with individual traits of dispersers and the demographic and ecological properties of destination colonies that are and are not selected in order to investigate the causes and predict the long-term consequences of dispersal (Nathan *et al.* 2008, Clobert *et al.* 2009).

We thank the National Trust (Farne Islands), Forth Seabird Group (Forth Islands), Scottish Seabird Centre (Craigleith and Fidra), Fair Isle Bird Observatory (Fair Isle), Royal Society for the Protection of Birds (Inchmickery), J. Bull (IoM), M. Frederiksen (IoM), M. Hall (IoM), M. Harris (IoM), M. Heubeck (Sumburgh Head), G. Leaper (Fowlsheugh), M. Newell (IoM), T. Reed (IoM), R. Sellers (Badbea), R.L. Swann (North Sutor), R. Duncan (Bullers of Buchan) and L. Wilson (IoM) for help with data collection and colour-ringing; Scottish Natural Heritage for access to the Isle of May National Nature Reserve; Isle of May Bird Observatory for providing BTO rings; D. Ferguson, B. Simpson, I. Watson and North 58˚ Sea Adventure Ltd. for boat services; the numerous observers who provided winter observations particularly R. Duncan; S. Cavers, R. Nager, M. Frederiksen and anonymous referees for thoughtful comments; and NERC (EJB) and the Royal Society (JMR) for funding.

REFERENCES

Aebischer, N.J. 1995. Philopatry and colony fidelity of shags, *Phalacrocorax aristotelis*, on the east-coast of Britain. *Ibis.* **137:** 11-18.

Aebischer, N.J., Potts, G. & Coulson, J. 1995. Site and mate fidelity of shags, *Phalacrocorax aristotelis*, at two British colonies. *Ibis*. **137:** 225-232.

Aebischer, N.J. & Wanless, S. 1992. Relationships between colony size, adult non-breeding and environmental conditions for shag *Phalacrocorax aristotelis* on the Isle of May, Scotland. Bird Study. **39:** 43-52.

Baker, M., Nur, N. & Geupel, G. 1995. Correcting biased estimates of dispersal and survival due to limited study area – theory and an application using wrentits. *Condor*. **97:** 663-674.

Broquet, T. & Petit, E. 2009. Molecular estimation of dispersal for ecology and population genetics. *Annu. Rev. Ecol. Syst*. **20:** 193-216.

Chambers, S. 1995. Spatial structure, genetic variation, and the neighbourhood adjustment to effective population size. *Conserv. Biol*. **9:** 1312-1315.

Chapman, D., Dytham, C. & Oxford, G. 2007. Modelling population redistribution in a leaf beetle: an evaluation of alternative dispersal functions. *J. Anim. Ecol*. **76:** 36-44.

Charmantier, A., Buoro, M., Gimenez, O. & Wiemerskirch, H. 2011. Heritability of short-scale natal dispersal in a large-scale foraging bird, the wandering albatross. *J. Evol. Biol.* **24:** 1487-1496.

Clobert, J., Danchin, E., Dhondt., A.A., & Nichols, J.D. 2001. *Dispersal*, Oxford University Press, UK.

Clobert, J., Le Galliard, J., Cote, J., Meylan, S. & Massot, M. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. *Ecol. Lett.* **12:** 197-209.

Cooper, C., Daniels, S. & Walters, J. 2008. Can we improve estimates of juvenile dispersal distance and survival? *Ecology.* **89:** 3349-3361.

Coulson, J.C. & Nève de Mévergnies, G. 1992. Where do young Kittiwakes *Rissa tridactyla* breed, philopatry or dispersal? *Ardea*, **80:** 187-197.

Doligez, B. & Pärt, T. 2008. Estimating fitness consequences of dispersal: a road to 'know-where'? Non-random dispersal and the underestimation of dispersers' fitness. *J. Anim. Ecol.* 77: 1199–1211.

Frederiksen, M. & Petersen, A. 1999. Philopatry and dispersal within a Black Guillemot colony. *Waterbirds*, **22:** 274-281.

Frederiksen, M., Daunt, F., Harris, M.P. & Wanless, S. 2008. The demographic impact of extreme events: stochastic weather drives survival and population dynamics in a long-lived seabird. *J. Anim. Ecol*. **77:** 1020-1029.

Galbraith, H., Baillie, S.R., Furness, R.W. & Russell, S. 1986. Regional variations int eh dispersal patterns of shags Phalacrocorax aristotelis in Northern Europe. *Ornis Scand*. **17:** 68-74.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Anim. Behav*. **28:** 1140-1162.

Greenwood, P.J. & Harvey, P. 1982. The natal and breeding dispersal of birds. *Annu. Rev. Ecol. Syst.* **13:** 1-21.

Hanski, I. 1999. *Metapopulation Ecology*, Oxford University Press, UK.

Harris, M.P. & Swann, R. 2002. European Shag (Shag) *Phalacrocorax aristotelis*. *The migration atlas: movements of the birds of Britain and Ireland* (eds C.V. Wernham, M.P. Toms, J.H. Marchant, J.A. Clark, G.M. Siriwardena & S.R. Baillie), pp. 139-142. T. & A.D. Poyser, London.

Hawkes, C. 2009. Linking movement behaviour, dispersal and population processes: is individual variation a key? *J. Anim. Ecol.* **78:** 894-906.

Hénaux, V., Bregnballe, T, & Lebreton, J.D. 2007. Dispersal and recruitment during population growth in a colonial bird, the great cormorant *Phalacrocorax carbo sinensis*. *J. Avian Biol.* **38:** 44-57.

661 **Inchausti, P. & Weimerskirch, H.** 2002. Dispersal and metapopulation dynamics of an
662 oceanic seabird, the wandering albatross, and its consequences for its response to
663 long-line fisheries. *J. Anim. Ecol*. **75:** 765-770.
664 **Joanes, D. & Gill, C.** 1998. Comparing measures of sample skewness and kurtosis. *J. Roy.*
665 *Stat. Soc. D-Stat*. **47:** 183–189.
666 **Kesler, D., Walters, J. & Kappes, J.** 2010. Social influences on dispersal and the fat-tailed
667 dispersal distribution in red-cockaded woodpeckers. *Behav. Ecol.* **21:** 1337-1343.
668 **Koenig, W., Van Vuren, D. & Hooge, P.** 1996. Detectability, philopatry, and the
669 distribution of dispersal distances in vertebrates. *Trends Ecol. Evol.* **11:** 514-517.
670 **Kot, M., Lewis, M. & van den Driessche, P.** 1996. Dispersal data and the spread of
671 invading organisms. *Ecology*. **77:** 2027-2042.
672 **Lawson-Handley, L. & Perrin, N.** 2007. Advances in our understanding of mammalian
673 sex-biased dispersal. *Mol. Ecol*. **16:** 1559-1578.
674 **Lowe, W.** 2010. Explaining long-distance dispersal: effects of dispersal distance on survival
675 and growth in a stream salamander. *Ecology*. **91:** 3008-3015.
676 **Lund, U. & Agostinelli, C.** 2011. circular: Circular Statistics. R package version 0.4-1.
677 http://CRAN.R-project.org/package=circular
678 **Matthysen, E., van de Casteele, T. & Adriaensen, F.** 2005. Do sibling tits (*Parus major, P-caeruleus*) disperse over similar distances and in similar directions? *Oecologia*.
680 **143:** 301-307.
681 **McCallum, H.** 2000. *Population parameters: estimation for ecological modelling*, Blackwell
682 Sciences, Oxford.
683 **Mills, L. & Allendorf, F.** 1996. The one-migrant-per-generation rule in conservation and
684 management. *Conserv. Biol*. **10:** 1509-1518.
685 **Nathan, R., Perry, G., Cronin, J., Strand, A. & Cain, M.** 2003. Methods for estimating
686 long-distance dispersal. *Oikos*. **103:** 261-273.
687 **Nathan, R., Getz, W., Refilla, E., Holyoak, M., Kadmon, R., Saltz, D. & Smouse, P.**
688 2008. A movement ecology paradigm for unifying organismal movement research.
689 *P. Natl. Acad. Sci. USA*. **105:** 19052-19059.
690 **Newell, M., Harris, M.P., Skene, A., Wanless, S. & Daunt, F.** 2010. *Isle of May seabird*
691 *studies in 2010*. JNCC Draft Report.
692 **Ollason, J.C. & Dunnet, G.M.** 1983. Modelling annual changes in numbers of breeding
693 fulmars, *Fulmarus glacialis*, at a colony in Orkney. *J. Anim. Ecol*. **52:** 185-198.

694 **Petrovskii, S. & Morozov, A.** 2009. Dispersal in a statistically structured population: fat-
695 tails revisited. *Am. Nat*. **173:** 278-289.
696 **Potts, G., Coulson, J. & Deans, I.** 1980. Population dynamics and breeding success of the
697 shag, *Phalacrocorax aristotelis*, on the Farne Islands, Northumberland. *J. Anim.*
698 *Ecol.* **49:** 465-484.
699 **R Development Core Team.** 2011. R: A language and environment for statistical
700 computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.R-
701 project.org.
702 **Rodenhouse, N., Sherry, T., & Holmes, R.** 1997. Site-dependent population regulation of
703 population size: a new synthesis. *Ecology*. **78:** 2025-2042.
704 **Serrano, D., Tella, J., Donázar, J. & Pomarol, M.** 2003. Social and individual features
705 affecting natal dispersal in the colonial lesser kestrel. *Ecology*. **84:** 3044-3054.
706 **Sharp, S., Baker, M., Hadfield, J., Simeoni, M. & Hatchwell, B.** 2008. Natal dispersal and
707 recruitment in a cooperatively breeding bird. *Oikos.* **117:** 1371-1379.
708 **Snow, B.** 1960. The breeding biology of the shag *Phalacrocorax* aristotelis on the island of
709 Lundy, Bristol Channel. *Ibis*. **102:** 554-572.
710 **Sonsthagen, S., Talbot, S., Lanctot, R. & McCracken, K.** 2010. Do common eiders nest in
711 kin groups? Microgeographic genetic structure in a philopatric sea duck. *Mol. Ecol*.
712 **19:** 647-657.
713 **Spear, L., Pyle, P. & Nur, N.** 1998. Natal dispersal in the western gull: proximal factors and
714 fitness consequences. *J. Anim. Ecol.* **67:** 165-179.
715 **Tavecchia, G., Minguez, E., de León, A., Louzao, M. & Oro, D.** 2008. Living close, doing
716 differently: small-scale asynchrony in demography of two species of seabird. *Ecology*.
717 **189:** 77-85.
718 **Wanless S. & Harris M.P.** 2004. European shag. Seabird Populations of Britain and Ireland.
719 (eds P.I. Mitchell, S.F. Newton, N. Ratcliffe, T.E. Dunn), pp. 146-159. T & A. D.
720 Poyser, London.
721 **Wanless, S., Harris, M.P. & Morris, J.** 1991. Foraging range and feeding locations of shag,
722 *Phalacrocorax aristotelis*, during chick rearing. *Ibis*. **133:** 30-36.
723 **Winkler, D., Wrege, P., Allen, P, Kast, T., Senesac, P., Wasson, M. & Sullivan, P.** 2005.
724 The natal dispersal of tree swallows in a continuous mainland environment. *J. Anim.*
725 *Ecol.* **74**: 1080-1090.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article.

Supporting Information **Appendix S1.**
Estimation of the total number of adult shags checked for colour-rings on the Isle of May and at other breeding colonies.

Supporting Information **Appendix S2.**
The degree to which incomplete detection of breeding adult shags on Isle of May or elsewhere might have caused estimated distributions of dispersal distances and directions to be biased.

Supporting Information **Appendix S3**
Winter roost sites surveyed for colour-ringed adult shags during 2008-2010, and winter locations of observed individuals.

Table 1. Colonies surveyed for breeding colour-ringed shags during 2008-2010 including; the maximum number of shags checked on one survey (Survey Maximum), the cumulative number of observations over all surveys at that colony (Total Observed), the total number of individual shags estimated to have been checked at that colony (Total Checked; Supporting Information Appendix S1), and the total number of colour-ringed adults located at that colony (Number Colour-Ringed). Colonies are listed by increasing distance away from the IoM (Distance (km)). *The IoM was surveyed throughout each breeding season (see Methods). Breeding colony size (Size) was categorised as 1 (<50 pairs), 2 (50-100 pairs) or 3 (≥100 pairs). N.B. The total number of individual shags checked at a colony (Total Checked) may be lower than indicated total breeding colony size.

Colony	Code	Distance (km)	Size	Number of Surveys 2008	Number of Surveys 2009	Number of Surveys 2010	Survey Maximum	Total Observed	Total Checked	Number Colour-Ringed
Isle of May, Firth of Forth	IoM	0	3	1*	1*	0	854	1511	938	416
Bass Rock, Firth of Forth	BR	13	1	0	1	0	20	20	20	0
Craigleith, Firth of Forth	CL	16	3	4	6	0	171	1053	239	3
The Lamb, Firth of Forth	LA	18	2	1	3	0	32	80	51	0
Fidra, Firth of Forth	FD	19	3	1	5	0	81	397	159	8
Inchkeith, Firth of Forth	IK	40	3	2	5	0	102	542	185	16
Car Craig, Firth of Forth	CC	48	1	1	0	0	24	24	24	0
Inchmickery, Firth of Forth	IM	49	2	3	4	0	120	527	182	2
Inchcolm, Firth of Forth	IC	50	1	1	0	0	11	11	11	0
St.Abbs Head, Berwickshire	SA	50	3	0	3	0	59	155	86	0
Arbroath, Angus	AB	60	1	0	3	0	31	74	38	2
Brownsman, Farne Islands	BM	98	3	2	3	0	156	381	206	1
East Wideopens, Farne Islands	EW	99	3	1	0	0	57	57	57	1
Inner Farne, Farne Islands	IF	99	3	3	1	0	396	851	479	0
Staple Island, Farne Islands	ST	99	3	2	3	0	83	317	146	2
Longstone End, Farne Islands	LS	100	1	1	0	0	32	32	32	1
Fowlsheugh, Kincardineshire	FH	105	2	1	4	0	47	190	179	3
Cove Bay, Aberdeenshire	CB	126	1	0	1	0	9	9	9	1
Bullers of Buchan, Aberdeenshire	BB	170	3	0	4	0	229	802	277	4
Troup Head coastline, Aberdeenshire	TC	217	3	1	2	0	299	716	411	0
Sandend, Banffshire	SE	250	1	4	1	0	36	121	51	0
Portknockie, Banffshire	PK	256	2	2	6	0	93	481	122	0
Flamborough Head, North Yorkshire	FM	355	1	0	2	0	15	23	19	0
North Sutor, Cromarty	NS	352	3	1	1	0	22	38	29	0
Badbea, Caithness	CN	437	3	1	1	0	96	181	123	0
Rousay, Orkney	RS	561	2	0	0	1	172	172	172	0
Fair Isle	FI	644	2	3	2	0	89	276	104	0
Sumburgh Head, Shetland	SM	689	3	0	2	0	65	118	76	0
Grand Total				35	63	1	3401	9159	4425	460

Figure legends

Figure 1 Location of **(a)** Isle of May (IoM) and 27 other breeding colonies and **(b)** 20 winter roost sites that were surveyed for colour-ringed Shags. Marker colour indicates colony size (see Table 1; white = size 1, grey = size 2, black = size 3). Colony codes are defined in Table 1.

Figure 2 (a) Proportional distribution of distances from natal to observed breeding site within Isle of May for 159 male and 126 female Shags, and the proportions of observed versus randomised dispersal distances (±SD) for **(b)** males and **(c)** females.

Figure 3 (a) Proportional distribution of directions from natal to observed breeding site within Isle of May for 159 male and 126 female Shags , and the proportions of observed versus randomised dispersal directions (±SD) for **(b)** males and **(c)** females.

Figure 4 Distributions of dispersal directions for **(a)** within Isle of May (IoM) **(b)** outside IoM and **(c)** within and outside IoM combined. Wedge size represents the number of Shags dispersing in a particular direction.

Figure 5 Total number of adult Shags estimated to have been checked at each colony away from Isle of May (primary y axis), and the total number of colour-ringed adult Shags observed at each colony (secondary y axis).

Figure 6 Overall distribution of observed dispersal distances both within and outside Isle of May. Note the break in the x-axis.

Fig.1.

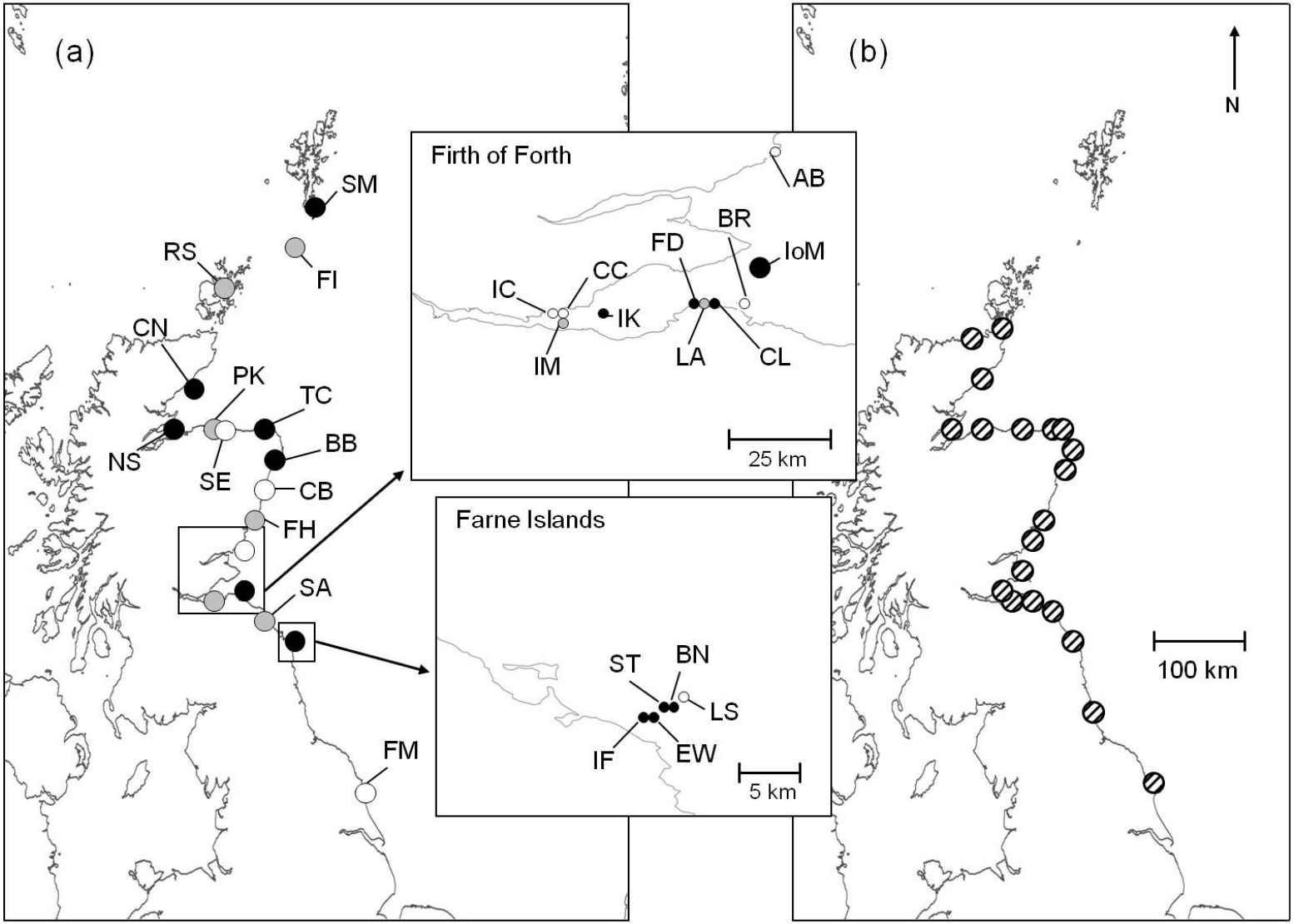

(a)
(b)
N
SM
FI
RS
CN
PK
TC
BB
NS
SE
CB
FH
SA
FM
Firth of Forth
AB
BR
FD
IoM
CC
IC
IK
IM
LA
CL
25 km
Farne Islands
ST
BN
LS
IF
EW
5 km
100 km

Fig.2.

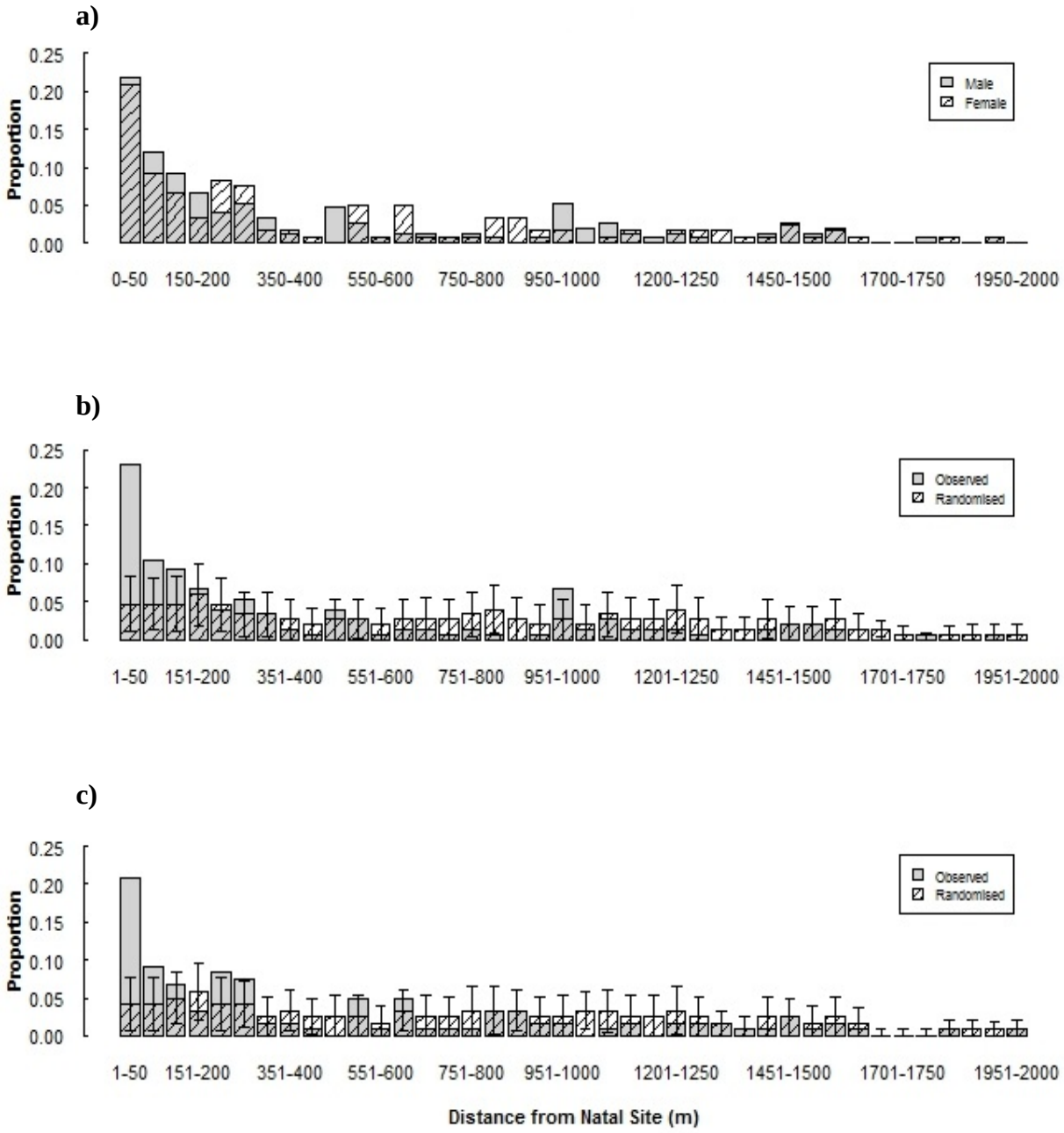

a)
Proportion
0.25
0.20
0.15
0.10
0.05
0.00
Male
Female
0-50
150-200
350-400
550-600
750-800
950-1000
1200-1250
1450-1500
1700-1750
1950-2000
b)
Proportion
Observed
Randomised
1-50
151-200
351-400
551-600
751-800
951-1000
1201-1250
1451-1500
1701-1750
1951-2000
c)
Proportion
Observed
Randomised
1-50
151-200
351-400
551-600
751-800
951-1000
1201-1250
1451-1500
1701-1750
1951-2000
Distance from Natal Site (m)

Fig.3.

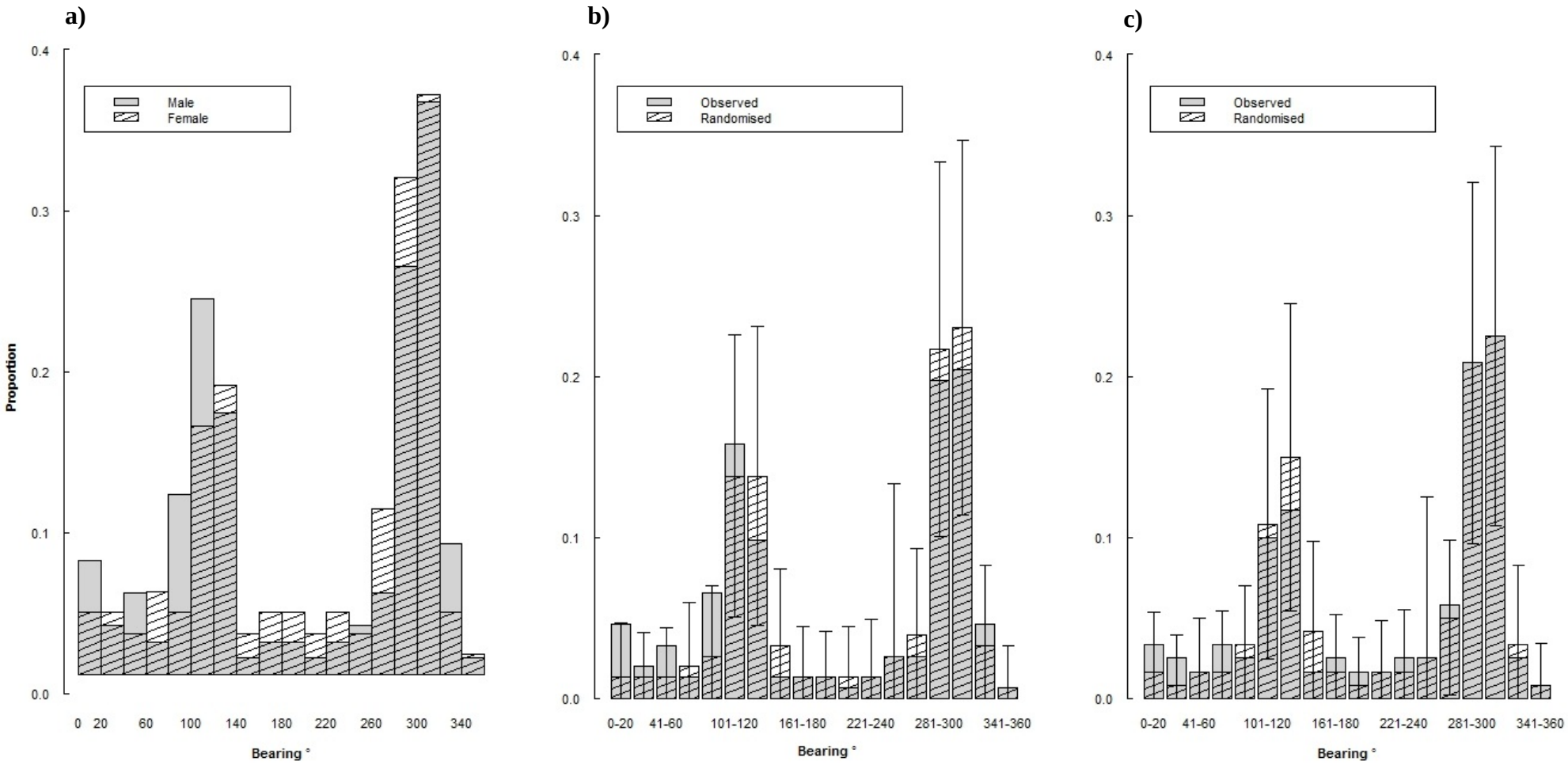

a)
b)
c)
Male
Female
Observed
Randomised
Proportion
0.0
0.1
0.2
0.3
0.4
0 20 60 100 140 180 220 260 300 340
0-20 41-60 101-120 161-180 221-240 281-300 341-360
Bearing °

Fig.4.

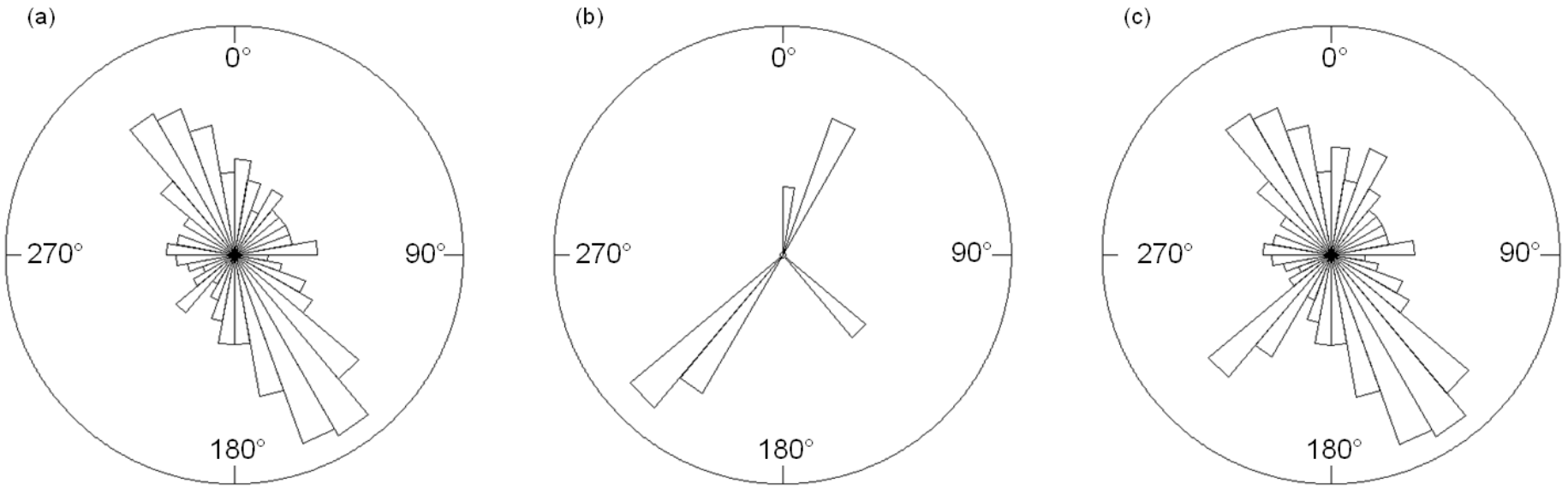


Fig.5.

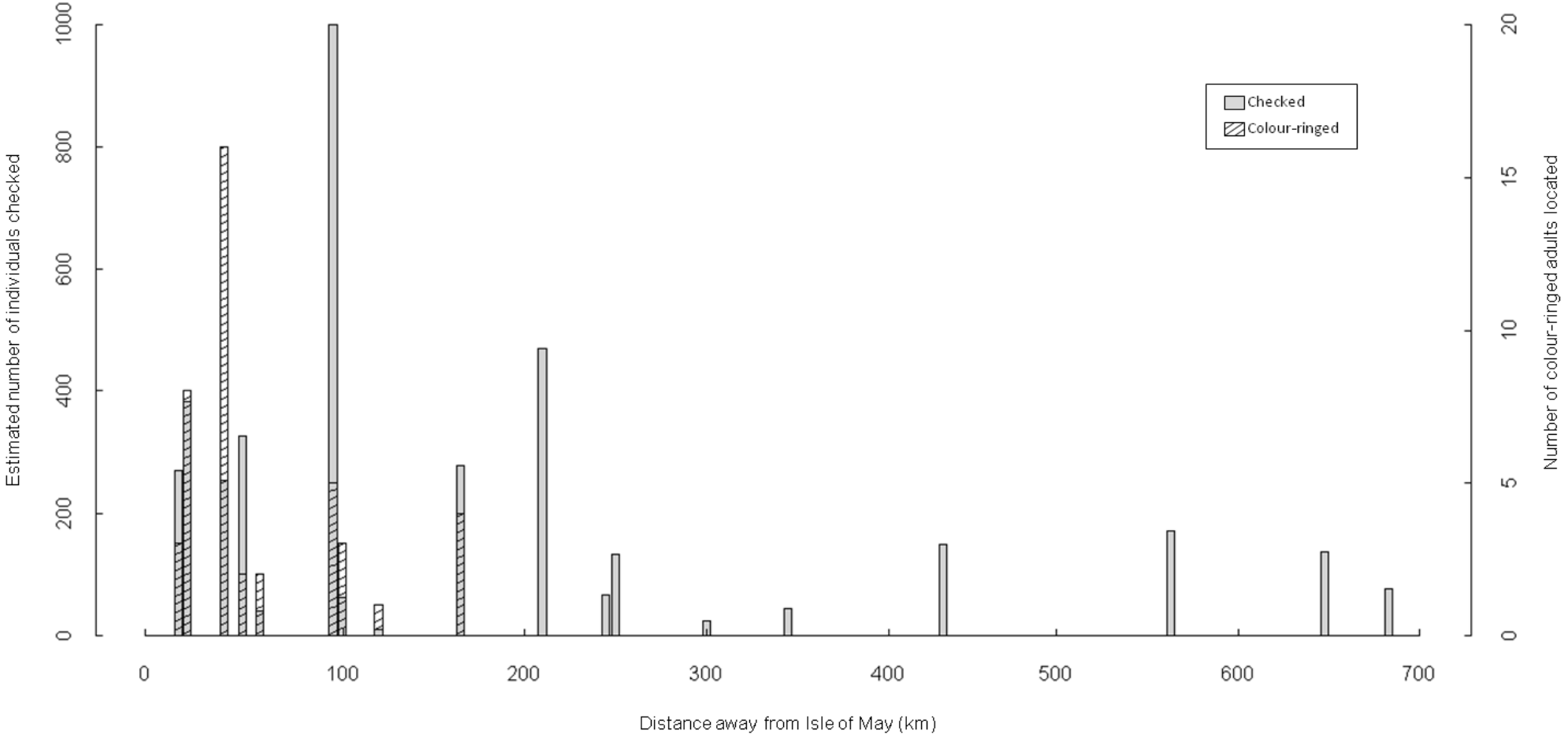
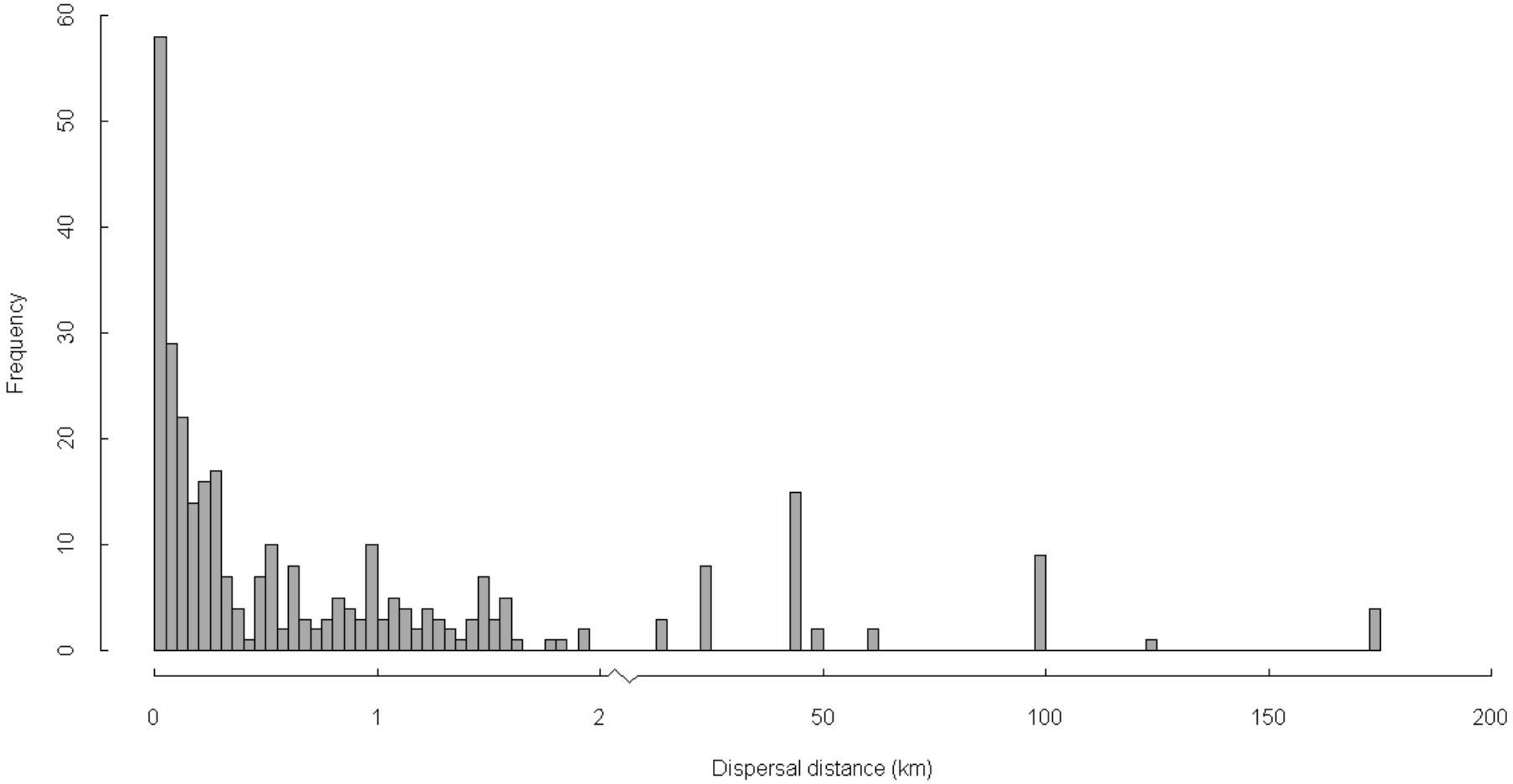

Checked
Colour-ringed
Estimated number of individuals checked
Number of colour-ringed adults located
Distance away from Isle of May (km)
0
200
400
600
800
1000
5
10
15
20
100
300
500
700

Fig.6.


Frequency
0
10
20
30
40
50
60
0
1
2
50
100
150
200
Dispersal distance (km)