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Breeding together, feeding apart: Sympatrically breeding seabirds forage in individually distinct locations

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Running page head Individual foraging behaviour

Abstract

Individuals can specialise such that mutually exclusive home ranges arise and the acquisition of site familiarity early in life can favour individual site fidelity in mature animals. Non-territorial Individual Foraging Site Fidelity (IFSF) has been reported frequently and among seabirds, foraging theory predicts that IFSF is more likely in

short-ranging, benthic foraging species, because their prey occur predictably at small scales. We tracked 17 adult and two immature black guillemots *Cepphus grylle* (mean mass 406g, median of individual maximum foraging range 4.3km). Individuals consistently returned to the same feeding areas, such that IFSF was significantly greater than the null expectation at spatial scales of 0.1 – 5 km and did not decay significantly over ten days. Immature birds ranged more widely than adult birds. Our study demonstrates that space use varies between individuals and that processes or threats occurring within the foraging range of a given colony may act disproportionately on some individuals rather than be equally distributed across a population. This finding contributes to a growing body of research on IFSF, which may have important implications for species management.

Keywords GPS, tracking, site fidelity, IFSF, roosting, black guillemot, specialisation, home range.

1. Introduction

Many established foraging theories assume that individuals within a species or population are ecologically equivalent (Fretwell & Lucas 1969). However, it is now recognised that individuals often specialise in their foraging behaviour or occupy only a small portion of the habitat potentially available to them (Bolnick et al. 2003, Piper 2011). It is well known that territorial animals, such as tigers (Sunquist 1981) and colonies of ants (Hölldobler and Lumsden 1980), establish discrete home ranges and maintain these through aggression and that territoriality therefore promotes foraging site fidelity. Latterly however, it has been also shown that many mobile, non-territorial, animals are also highly consistent in where and how they forage, at the individual level (Ceia & Ramos 2015). That is, individual foraging site fidelity (IFSF) – when individuals consistently forage in only a small part of their population's home range – is higher than the null expectation. This form of individual specialisation has been shown even among colonial central-place foragers, such as pinnipeds (Baylis et al. 2012) and seabirds (Harris et al. 2014, Baylis et al. 2015, Wakefield et al. 2015), which share common breeding or resting places, and might therefore be expected to share common foraging areas. High IFSF has important implications for our understanding of these groups. For example, conservation mangers may need to account for the fact that potential threats, such as offshore windfarm developments or conversely protection measures, such as Marine Protected Areas, impact individuals within populations asymmetrically. The current challenge is therefore to detect IFSF and understand why it occurs.

Several theories have been proposed to explain how individual foragers select foraging locations. The ‘Win-stay, lose-shift’ strategy (Kamil 1983, Davoren et al. 2003) proposes that birds revisit areas where previous foraging was successful until they encounter poor foraging success, after which they seek a new foraging area. The ‘Information centre hypothesis’ (Ward & Zahavi 1973) suggests that individuals may locate such areas using ‘public’ information gained from other birds at the colony. For example, they might emulate the bearing of other birds leaving the colony. The ‘Always stay’ strategy (Switzer 1993), suggest that animals gain a fitness advantage by consistently feeding in an area where they have previous experience or ‘private’ information (referred to as ‘site familiarity’ (Irons 1998, Piper 2011)). Both the win-stay, loose-shift and always stay strategies assume that birds have the capacity to memorise and evaluate patch location and/or quality (Benhamou 1994). Birds using the win-stay, loose shift strategy would be expected to exhibit high IFSF in the short term, but this would decline over time. Always-stay foragers would have high IFSF regardless of time scale. A simpler strategy, not reliant on memory, would be to search for prey anew each time the bird left the colony. This would result in low IFSF. Theory predicts that IFSF should be highest when prey availability is most predictable (Weimerskirch 2007). Seabirds are a diverse group and vary in the degree of predictability in the environments in which they feed. Tropical and wide-ranging pelagic species, and those that forage at oceanic fronts experience relatively less predictable environments than temperate, polar, neritic, coastal and short-ranging species (Weimerskirch 2007).

The collection of seabird tracking data has mushroomed with the availability of affordable tracking technology (Lascelles et al. 2016, Wakefield et al. 2017) but some species and age classes remain elusive to tracking because either their size or behaviour prevents them from being tracked. Immature age classes are also less frequently the subject of tracking studies (Votier et al. 2017) but younger age classes are predicted to show less IFSF and more prospecting behavior as they explore potential feeding and breeding locations and then use memory-based learning to concentrate their selection with experience (Guilford et al. 2011, Wakefield et al. 2015). One species which has rarely been tracked is the black guillemot (*Cepphus grylle*) which, like some other crevice breeding alcids, can be sensitive to capture, causing low recovery rates of devices (Harris et al. 2012, Masden et al. 2013, Shoji et al. 2015). In temperate regions this species also forages towards the most predictable end of the spectrum of foraging habitats (Ewins 1990). Their main prey in our study region is butterfish (*Pholis gunnellus*; Ewins 1990; Walton 2004) which occupy static habitat features (kelp and rocky subtidal zones), only moving offshore to spawn during December (Sawyer 1967). Koop and Gibson (1991) showed that butterfish are sedentary, moving an average of only 21m in 6 days. In the same study, butterfish returned to an area within two tidal cycles of their removal, although numbers were reduced to 27–52% of the initial population. In temperate populations, black guillemots remain close to their breeding colonies for the whole year and forage over short distances (Ewins 1990).

We use novel field methods and high-precision global positioning systems (GPS) telemetry to track individual breeding adult and colony-attending immature black

guillemots to (1) determine whether IFSF occurs; (2) whether IFSF declines over time; and (3) whether it is higher in adults than immatures.

2. Material and Methods

2.1 Data collection

Our study colony, Grassholm, is a three-hectare island (59.06° N, 2.93° W) lying in a shallow channel between the mainland of Orkney and the island of Shapinsay in Northern Scotland. Surveys recorded 13 black guillemots at the colony in 1984 (Lloyd et al. 1991) and three nests in 1991, all located in natural crevices (P. Hollinrake, unpubl. data). In 1996, artificial stone nesting cairns were built and by 2000, 50 individuals were counted on land (Mitchell et al. 2004). The current population is approximately 60 breeding pairs, 80-90% of which use artificial nesting cairns. The surrounding water is shallow (<15m depth) with areas of sandy and rocky seabed, the latter densely covered in fucoid algae.

Black guillemots are burrow or cavity nesters. Due to concern that they may abandon breeding or evade recapture if caught from the burrow by hand, tagged, and then recaught a few days later to retrieve the tag (Masden et al. 2013, Shoji et al. 2015), we caught birds primarily by intercepting those entering or leaving the colony using a mist net positioned between 2 and 20m from the colony edge. We used remote download tags which negated the need to recapture birds since we expected tags to be shed after 10-20 days. Two birds were caught in the burrow and one of these recaught to remove the tag and check for signs of damage to plumage

or skin. Immature black guillemots, which attend colonies in small numbers, were distinguishable from adults based on plumage characteristics (Cramp 1985).

Following capture, we attached an Ecotone Uria GPS tag, weighing 11g including attachment material. This is ~ 2.8 % body mass (range 2.4 - 3.1 %), and therefore generally below the mass thought to have an acceptably small effect on bird behaviour (Phillips et al. 2003, Schacter and Jones 2017). We attached tags to the feathers on the lower back, just below the widest part of the body, using 3 strips of tesa tape (Tesa, Norderstedt, Germany). We used this position, rather than mounting between the wings, to reduce the likelihood of tags impeding birds as they passed through burrow entrances. We programmed tags to record one GPS position every 10 minutes and expected battery life to be 5 - 10 days and fitted birds with a field-readable colour ring with a unique 2-letter combination. Birds were released within 6 minutes of capture. Archived data were downloaded automatically from the tags to a base station via a VHF link whenever birds were within 1 km. Examination of the attachment location of the bird re-caught by hand revealed no visible ill effects. Black guillemots are synchronous breeders at the colony (Cramp 1985). Therefore, where nest locations of tagged birds where not known we assumed the adults where either incubating eggs or brooding chicks, depending on observations of the breeding state of the population as whole, which is easily observed at this colony. In 2013, three tags were deployed on adults and one on an immature in June when the population were incubating eggs and four tags were deployed on adults and one on an immature in July during brooding. In 2014, 13 tags were deployed on adults in July during brooding.

We monitored breeding success on the island over five visits spanning the breeding season in 2013, during which the contents of all nests on the island were recorded. In 2014, we completed one visit in late chick rearing to record the number of chicks expected to fledge. During all visits to the colony we noted prey species being carried by chick-provisioning black guillemots opportunistically.

2.2 Analysis

The GPS loggers tended to omit locations during birds' dives. To ensure a constant 10-minute interval between locations, we re-sampled tracks by linear interpolation. Exploratory analysis showed that speeds were binomially distributed. Some birds frequently roosted on fixed objects, such as buoys and rocks, outside the study colony, and some visited neighbouring colonies, in addition to their own (see Results). We identified all potential roosting features using Admiralty navigation charts, Google Earth and the Seabird 2000 colony database (Mitchell et al. 2004). We classified birds' locations as *roosting* when they were within a minimum distance of the centre of those features (where distance was defined separately for each feature depending on its size and type – see Table S1) and their speed was < 0.5 m/s. All remaining locations were classified as *at-sea*. Tortuosity at each location L_0 was the straight-line distance between L_{-1} and L_1 divided by the distance between L_{-1} and L_1 passing through L_0, and was binomially distributed. All locations defined as 'at-sea' were classified as putative foraging locations if tortuosity was ≤ 0.9. We defined foraging trips as sets of contiguous locations >250 m from the study colony spanning ≥ 20 minutes, due to the temporal resolution of the tracking data it was not be possible to detect shorter trips.

We estimated each individuals' 50% foraging utilisation distribution (UD) by calculating the kernel density of foraging locations on a regular 100 m grid, with a smoothing factor (*h*) of 50 m (Worton 1989). The apparent degree of overlap between UD contours estimated using this technique is sensitive to both the percentage contour chosen and *h*, which effectively sets the spatial scale of the analysis. Therefore, to test whether IFSF was greater than expected by chance, we developed a multi-scale approach, based on comparing individual UDs for different periods, as described by Wakefield et al. (2015). We confined this part of our analysis to 2014, when most data were collected. Wakefield et al. (2015) compared the UDs of gannets tracked across consecutive foraging trips at two-minute resolution. Exploratory analysis showed that too few tracking locations were recorded in each foraging trip to estimate UDs reliably at this level, because foraging trip length was short relative to the tracking interval (see Results). We therefore calculated UDs for each day, *d*, as our unit of analysis. To do so, we first transformed the locations of black guillemots to Lambert Azimuthal Equal Area projection. We then overlaid a grid in this projection, centred on the study colony, comprising *x* hexagonal cells with centres spaced *s* m apart. We next calculated $\hat{UD}_{i,d}$ at each grid cell as the proportion of the *i*th individual's locations on the *d*th day falling in that cell. For each individual, we then picked two daily UDs at random and calculated the Bhattacharyya's affinity, *BA*, between them, where

$$BA_i = \sum_{\mathrm{All}x} \sqrt{\hat{UD}_{i,1}(x)\hat{UD}_{i,2}(x)} \qquad (1)$$

In this case, *BA* quantifies the similarity between the UDs of the bird on the two days and ranges from 0 (no spatial consistency) to 1 (perfect spatial consistency) (Fieberg & Kochanny 2005, Wakefield et al. 2015). We then calculated BA_{obs}, the median *BA* across individuals. We tested the hypothesis that this is greater than the median similarity expected under the null hypothesis that bird identities are exchangeable, BA_{null}. If this hypothesis is rejected, individuals consistently occupy only a small proportion of their population's home range, which is equivalent to the well-known definition of individual specialisation (Bolnick et al. 2002). To determine the distribution of BA_{null}, we repeated the above procedure 10000 times, randomly reassigning bird identities without replacement at each iteration. We then calculated the exact probability that $BA_{obs} > BA_{null}$ as $p = (b+1)/(m+1)$, where b is the number of instances where $BA_{null} > BA_{obs}$ and m is the number of iterations (Phipson and Smyth 2010). As the spatial scale at which UDs are discretised on a grid increases, those UDs will inevitably become more similar. To check how scale affected the test, we repeated it 11 times, on grids with cells spacing of $s = \{100, 150, 225, \ldots, 5767\}$ i.e. s ranged from 100 m to approximately two thirds of the maximum foraging range that we observed (see Results).

To determine whether birds used a win-stay, lose-shift strategy within the study period we tested whether spatial consistency decayed over time. To do so, we calculated BA_t (on a grid with s = 1 km) for each bird by substituting the UDs of that bird on day two and day t into equation 1 above. Day two was chosen as the reference day, rather than day one, in case the behaviour of birds was initially

affected by tag attachment. We then modelled BA_t as a function of lag using a generalised linear mixed model (GLMM) fitted in the R package nlme (Pinheiro et al. 2016). We arcsine transformed BA_t to improve normality and specified correlated random slopes and intercepts for individuals. Both this and the previous analysis was carried out firstly on all at-sea locations and secondly on putative foraging locations only. Lag *t* ranged from 1 to 9 days (data were obtained from only one individual at greater lags).

3. Results

3.1 Summary of data

We successfully downloaded GPS data from 19 of 23 (83%) tags deployed (Table 1; Figure S1). The average tracking period was 8.4d (1-17d). In 2013, we caught and tagged two immature, first summer birds - one in June and the other in July. The remainder of tagged birds were assumed to be breeding adults. This assumption was supported by the fact that all birds had visible brood patches and commuted repeatedly to and from the colony (Fig. S1). We were able to monitor the nests of five of the eight breeding adults tagged in 2013 (Table 1). At three of these nests, birds were caught by mistnet and later observed entering or exiting nests. At the other two, the bird was originally caught on the nest, during incubation. The two nests where birds were caught had lower productivity than the three nests where birds were caught in a mistnet, where all three nests fledged the maximum of two chicks. Opportunistic observations of prey were dominated by butterfish but shanny (*Lioophyrys pholis*) and sea scorpion (*Taurulus bubulis*) were also observed.

252

253 **3.2 Individual foraging site fidelity**

254 Black guillemots foraged within a maximum distance from the colony of 8.04km
255 (Median1.7 km, Inter Quartile Range 3.6 - 5.88 km; 10.1km avoiding land; Table 2;
256 Figure S2). Both tracks (Figure 1; Figure S1) and 50% utilization distributions of
257 putative foraging locations (Figure 2) show that there was little overlap among the
258 core areas used by individuals. The 50% UDs were small showing that individuals
259 concentrated their foraging into a few small areas. Home ranges in 2013 were on
260 average slightly larger than in 2014 but the difference between group means by was
261 not statistically significant (one-way ANOVA: $F(1,15) = 2.497$, $p = 0.135$). Neither
262 tag duration (Estimate = 0.023, p =0.175), year (Estimate = 0.000, p = 0.999), nor
263 breeding stage (Estimate = 0.007, p = 0.968) were significant predictors of home
264 range area (linear model: Adjusted R-squared = -0.03325, F= 0.8069, df = 3,15, p=
265 0.5094).

266

267 IFSF increased with spatial scale (Table 2). When all locations were considered,
268 IFSF was significantly greater than the null expectation at all scales considered (i.e.
269 $BA_{obs} > BA_{null}$), other than 5.8 km. When only putative foraging locations were
270 considered, IFSF was significantly greater than the null expectation at all scales. The
271 gradient of IFSF with temporal lag did not differ significantly from zero, indicating that
272 IFSF did not decay significantly with time over a period of ten days (Table 3, Figure
273 3).

274

The two immature birds behaved somewhat differently to adults (Figure 2). IFSF was lower for immatures than adults at all but the smallest (100m grid) of the 11 scales tested (Table S2). One immature (tag 47), tracked during July, when adults were chick-rearing, ranged more widely than adults and the second (tag 29), tracked during June when adults are incubating, visited different colonies, perhaps prospecting for a breeding site or partner.

Twelve of the 19 individuals (including the two immature birds) roosted on buoys, fish farm cages (including those not currently stocked with fish), other colonies or rocks while away from the colony (Figure 4) and all available man-made objects (buoys and fish farms) within the observed foraging range were visited by one or more of the tracked black guillemots.

4. Discussion

Variation in the space use among individuals affects how populations are distributed and how they are affected by natural and anthropogenic impacts. It is becoming clear that individual foraging site fidelity occurs in many seabird species, yet it remains poorly characterised, especially among small, short ranging species and immatures (Ceia & Ramos 2015). We found that breeding black guillemots exhibited IFSF even at small spatial scales (500m) over up to 10 days, while foraging close to the colony, in shallow waters between islands, where resources were presumed to be relatively spatiotemporally predictable. In line with predictions of the exploration-refinement hypothesis, two immatures showed less IFSF than adults.

Our study adds black guillemot to the list of species including penguins, albatrosses, shearwaters, gulls, gannets, shags, cormorants and other auks (reviewed in Ceia & Ramos 2015), where IFSF has been documented during the breeding season and, along with these previous studies, makes the generalization that seabirds forage on unpredictably distributed prey (Lack 1968) seem overly simplistic. For example, IFSF in Northern gannets (*Morus bassanus*) breeding on Bass Rock, Scotland, persisted not only within but across breeding seasons. Most individuals foraged in consistent areas over time, though some were highly inconsistent (Wakefield et al. 2015). These gannets were feeding in wider variety of habitats than the black guillemots in our study, including more dynamic thermal front areas and less productive offshore waters. They were also feeding on schooling prey as opposed to the sedentary species black guillemots prefer. In the shallow waters surrounding the Orkney archipelago, the highly regular actions of the tides and daylight are likely to result in a much more predictability structured prey field than in more pelagic environments. In turn, this is likely to favour individual foraging site fidelity. The finding that black guillemots show IFSF even at very small spatial scales accords with expectations that a species feeding in a predictable environment should profit from repeatedly feeding in a preferred area (Weimerskirch 2007).

Comparing the degree of IFSF quantitatively between species from published accounts is currently complicated by the wide variety of methods used to quantify IFSF (Piper 2011). For example, the mean BA of gannet home ranges reported by Wakefield et al. (2015) was around 0.4 which was lower than the typical BA for black guillemots, but the scale at which IFSF is compared across these two species differs, making the comparison invalid. It would be useful for studies to describe the level of

IFSF at different spatial scales so that the resultant curves could be compared across species or populations (Figure S3). Comparing IFSF across species and populations could identify factors and mechanisms resulting in animals adopting IFSF strategies. In our study, IFSF did not decrease over the tracking period. This could be regarded as evidence that they used an 'always stay' rather than a win-stay, loose-shift strategy. However, our observation period was relatively short (<2 weeks). Moreover, the gradient of IFSF with time was negative and approached significance for the foraging locations-only model and the slopes for most individuals were negative. Therefore, while we did not observe a significant decay in IFSF over this period, win-stay, loose-shift foraging may occur over a longer timescale.

A key advantage of IFSF for black guillemots is likely to be increased site familiarity (Piper 2011). Short ranging results in short return times to prey patches over successive visits. Because little time has elapsed, prey conditions are less likely to vary between trips, favouring repeated visits to the same location (Weimerskirch 2007). Compared to the environments many seabirds forage in, black guillemot foraging areas are characterised by rocky, shallow substrates and tidal races. The former are static and offer physical features that individuals could learn to associate with prey. The latter are highly dynamic but predictable in time and space so that individuals could learn that at particular tidal states and locations certain types of prey would be likely to be found. These factors together favour the premium added by accruing local knowledge.

Riotte-Lambert et al. (2015) demonstrated that the ability of birds to evaluate and memorise patch quality could theoretically lead to IFSF. The idea that long-lived seabirds have the capacity to remember where and when prey become available is increasingly well supported (Ceia & Ramos 2015). For example, kittiwakes repeatedly chose specific areas and tidal stages for foraging suggesting that they can predict prey resources in both space and time (Irons et al 1998). The capacity for black guillemots in this study to evaluate patch quality would seem to be high because of their short ranging tendencies and static foraging habitats.

The two immatures we tracked showed less IFSF than adults, presumably because their behaviour was more exploratory. Apparent exploratory behaviour in immatures has now been reported in several seabird species (e.g. Guilford et al. 2011, Votier et al. 2017) with foraging choices narrowing in later life. Conservation managers therefore need to consider that threats such as pollution or development are likely to impact age classes differently, with younger age classes likely to be exposed to a lower level of impact but across a larger number of birds than older adults using IFSF.

From a conservation biology perspective, the discovery that a species exhibits IFSF changes its management because there is a shift from a situation in which individuals are exposed equally to a risk (e.g. from pollution, bycatch or industrial development) to one in which some individuals are exposed disproportionately. Moreover, IFSF suggests that foragers do not necessarily choose the optimal habitat from those available, violating a key assumption of the Ideal Free and Ideal Despotic

models (Fretwell & Lucas 1969), two of the benchmark theories in foraging ecology that are used by conservation managers (Boyd et al. 2018). Occurrence of IFSF also implies that the behaviour of individuals, such as successive choices about where and when to forage, may not be independent, even at wide temporal lags. This will result in strong within-individual temporal autocorrelation in for example tracking data, that must be accounted for when modelling habitat selection. A related advantage to both researchers and study animals, of high IFSF, is that the usage of an individual can be characterised by observing that individual for a relatively short period of time. In turn this may make it practicable to track more individuals, thereby leading to better predictions of space use (Wakefield et al. 2017). However, planning to protect the average of a population may actually harm the specialists within it (Bolnick et al. 2003), affecting populations particularly if those specialists are a demographically important part of the population. Specialists have been shown to have higher reproductive output than generalists in some seabird populations. For example, Pigeon guillemots *Cepphus columba* feeding a specialist diet had higher breeding success and fed larger prey items than generalists (Golet et al. 2000) and black-browed albatrosses *Thalassarche melanophris* which were more faithful between years to a foraging location had higher reproductive success than non-specialists (Patrick & Weimerskirch 2017).

The frequent observations of roosting in this species invites further investigation. Mandt's Black guillemots (*Cepphus grylle mandtii*) have also been observed to roost frequently though this was outside the breeding season and mostly at night on sea ice (Divoky et al. 2016). Our observations of birds resting on buoys etc. may have been due to birds attempting to save energy. For example, canvasback ducks

(*Aythya valisineria*) resting in water of 35°C have a metabolic rate of 4kcal/hr whereas in air of the same temperature the rate is 2.7kcal/hr. In colder water of 0°C the metabolic rate was much higher at 10.5kcl/hr (Alisauskas and Ankney, 1992). Roosting may also allow self-feeding (as opposed to chick feeding) birds to rest outside the colony between foraging bouts (Schreiber & Chovan 1986) or roosting sites could offer a vantage point from which to socialise or monitor the foraging behaviour of other birds (i.e. to gather public information). Ward & Zaharvi (1973) propose that communal roosts serve as information centres giving birds knowledge of local feeding resources, but individual black guillemots appear to segregate feeding areas rather than feed communally. It is also possible that black guillemots alight on structures outside the colony to stay stationary while waiting for favourable foraging conditions e.g. particular tidal states. Black guillemots could also use roosting sites to display or even defend a feeding territory. Such behaviour is almost unknown among seabirds (Drury & Smith 1968) but was observed anecdotally in one pair of pigeon guillemots (*Cepphus columba*) in Alaska (Kathy Kuletz *pers comm*). The fact that black guillemots appear to have a high propensity to roosting on man-made objects is relevant to their conservation, particularly where devices which present a potential collision risk, such as tidal turbines (Furness et al. 2012, Masden et al. 2013), are placed close to colonies. Such devices should be designed with limited space for roosting to ensure that black guillemots are not attracted to installations with moving parts.

We demonstrate that individual foraging site fidelity is a strong determinant of space use in a small, locally foraging seabird and that roosting away from the colony was common. Both these factors should be considered when designing spatial

conservation measures or assessing the potential impacts of developments such as tidal energy devices. Individuals cannot be assumed to be ecologically equivalent. Instead, the population-level consequences of threats or ecological processes act through a filter of individual variation.

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549 **Tables**

550 Table 1: The number of black guillemots tracked each year, duration of tracking,
551 breeding status and foraging range. Tags with zero days deployment were those that
552 never re-established contact with the base station either because the tag failed or
553 because the bird removed the tag or was absent from the colony. *On nest for
554 deployment and a second time to remove device.

Year	Bird ID (logger number in brackets)	Breeding status	Days of deploy-ment	Max Foraging range (km)	Capture method	Nest success at end of season (nest site number)
2013	25/AA (6)	Inc. adult	6	4.38	On nest	1 chick (nest 22)
2013	26/AB (13)	Inc. adult	4	3.40	Mistnet	2 chicks (nest 42)
2013	27/AC (5)	Inc. adult	0	No data	Mistnet	2 chicks (nest 9)
2013	29/AD (4)	Imm.	8	3.38	Mistnet	Non breeder
2013	32/AI (7)	Inc. adult	5	7.45	On nest*	Failed (nest 4)
2013	43/BV (25)	Brood. adult	5	4.62	Mistnet	Unknown
2013	44/BX (18)	Brood. adult	1	1.88	Mistnet	Unknown
2013	45/BZ (21)	Brood. adult	0	No data	Mistnet	2 chicks (nest 350)
2013	46/CA (17)	Brood. adult	1	3.94	Mistnet	Unknown
2013	47/CB (23)	Imm.	8	6.99	Mistnet	Non breeder
2014	01/DJ (2)	Brood. adult	10	7.27	Mistnet	Unknown
2014	02/DK (3)	Brood. adult	0	No data	Mistnet	Unknown
2014	03/DL (4)	Brood. adult	8	3.88	Mistnet	Unknown
2014	04/DN (5)	Brood. adult	8	5.12	Mistnet	Unknown

2014	32/AI (6)	Brood. adult	0	No data	Mistnet	Unknown
2014	10/DX (7)	Brood. adult	2	4.01	Mistnet	Unknown
2014	11/DZ (8)	Brood. adult	3	2.88	Mistnet	Unknown
2014	12/FA (9)	Brood. adult	9	3.39	Mistnet	Unknown
2014	13/FB (10)	Brood. adult	3	4.48	Mistnet	Unknown
2014	14/FC (11)	Brood. adult	10	5.29	Mistnet	Unknown
2014	15/FD (12)	Brood. adult	10	6.47	Mistnet	Unknown
2014	16/FF (14)	Brood. adult	7	8.04	Mistnet	Unknown
2014	17/FH (18)	Brood. adult	17	3.80	Mistnet	Unknown

555

Table 2: Observed (BA_{obs}) and null (BA_{null}) Bhattacharya's Affinity (BA) scores comparing within-individual consistency in foraging areas against between-individual consistency. A randomisation procedure tests the hypothesis that the median observed BA is <= than the null median BA. Individual consistency is high if median BA_{obs} is > the 95th percentile of median BA_{null}. Other percentiles of BA_{null} describe the shape and range of the null distribution and P is the probability that BA_{obs} is ≤ BA_{null}.

Subset	Scale (km)	N birds	Median BA_{obs} (min, max)	Percentiles of median BA_{null}				P
				25th	50th	75th	95th	
All locations at sea	0.100	11	0.10 (0.00, 0.37)	0.00	0.00	0.00	0.02	<0.001
	0.150	11	0.23 (0.00, 0.58)	0.00	0.00	0.02	0.05	<0.001
	0.225	11	0.29 (0.00, 0.66)	0.00	0.02	0.04	0.09	<0.001
	0.338	11	0.36 (0.14, 0.81)	0.03	0.05	0.08	0.15	<0.001
	0.506	11	0.51 (0.11, 0.88)	0.07	0.10	0.14	0.23	<0.001
	0.759	11	0.62 (0.14, 0.91)	0.13	0.16	0.27	0.36	<0.001
	1.139	11	0.66 (0.39, 0.92)	0.25	0.31	0.39	0.45	<0.001
	1.709	11	0.64 (0.31, 0.95)	0.40	0.46	0.52	0.57	<0.001
	2.563	11	0.79 (0.47, 0.93)	0.57	0.60	0.64	0.69	<0.001
	3.844	11	0.83 (0.56, 1.00)	0.73	0.76	0.78	0.83	0.018
	5.767	11	0.89 (0.47, 1.00)	0.82	0.89	0.89	0.89	0.110

Foraging locations	0.100	10	0.02 (0.00, 0.27)	0.00	0.00	0.00	0.00	<0.001
	0.150	10	0.13 (0.00, 0.34)	0.00	0.00	0.00	0.00	<0.001
	0.225	10	0.23 (0.00, 0.49)	0.00	0.00	0.00	0.00	<0.001
	0.338	10	0.42 (0.00, 0.67)	0.00	0.00	0.00	0.07	<0.001
	0.506	10	0.47 (0.00, 0.67)	0.00	0.00	0.05	0.12	<0.001
	0.759	10	0.60 (0.00, 0.90)	0.03	0.08	0.14	0.24	<0.001
	1.139	10	0.66 (0.18, 0.96)	0.09	0.18	0.25	0.37	<0.001
	1.709	10	0.69 (0.36, 0.94)	0.32	0.39	0.44	0.53	0.001
	2.563	10	0.80 (0.51, 0.99)	0.49	0.55	0.61	0.68	<0.001
	3.844	10	0.90 (0.60, 1.00)	0.69	0.72	0.76	0.83	0.002
	5.767	10	1.00 (0.58, 1.00)	0.86	0.92	0.94	0.97	<0.001

570 Table 3. Generalised Linear Mixed Models of similarity between the utilisation
571 distributions of individual black guillemots (BA_t) separated by a lag of *t* days as a
572 function of *t*.

Data set		Estimate	S.E.	*t*	p
All locations	Intercept	1.09	0.05	20.534	<0.001
	Slope	-0.02	0.02	-1.376	0.175
Foraging locations	Intercept	1.03	0.09	12.185	<0.001
	Slope	-0.04	0.02	-1.710	0.093

573

Figures

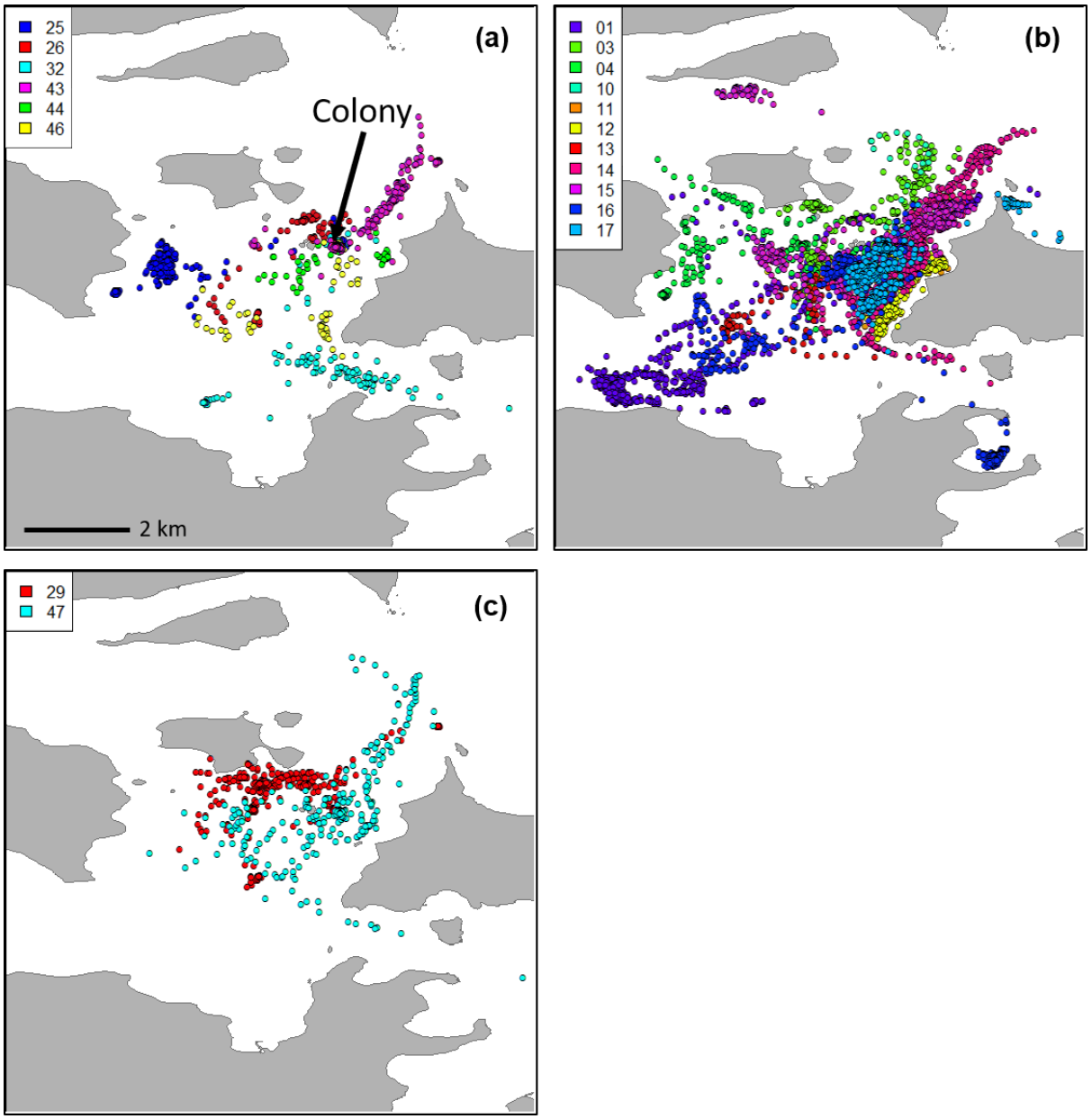
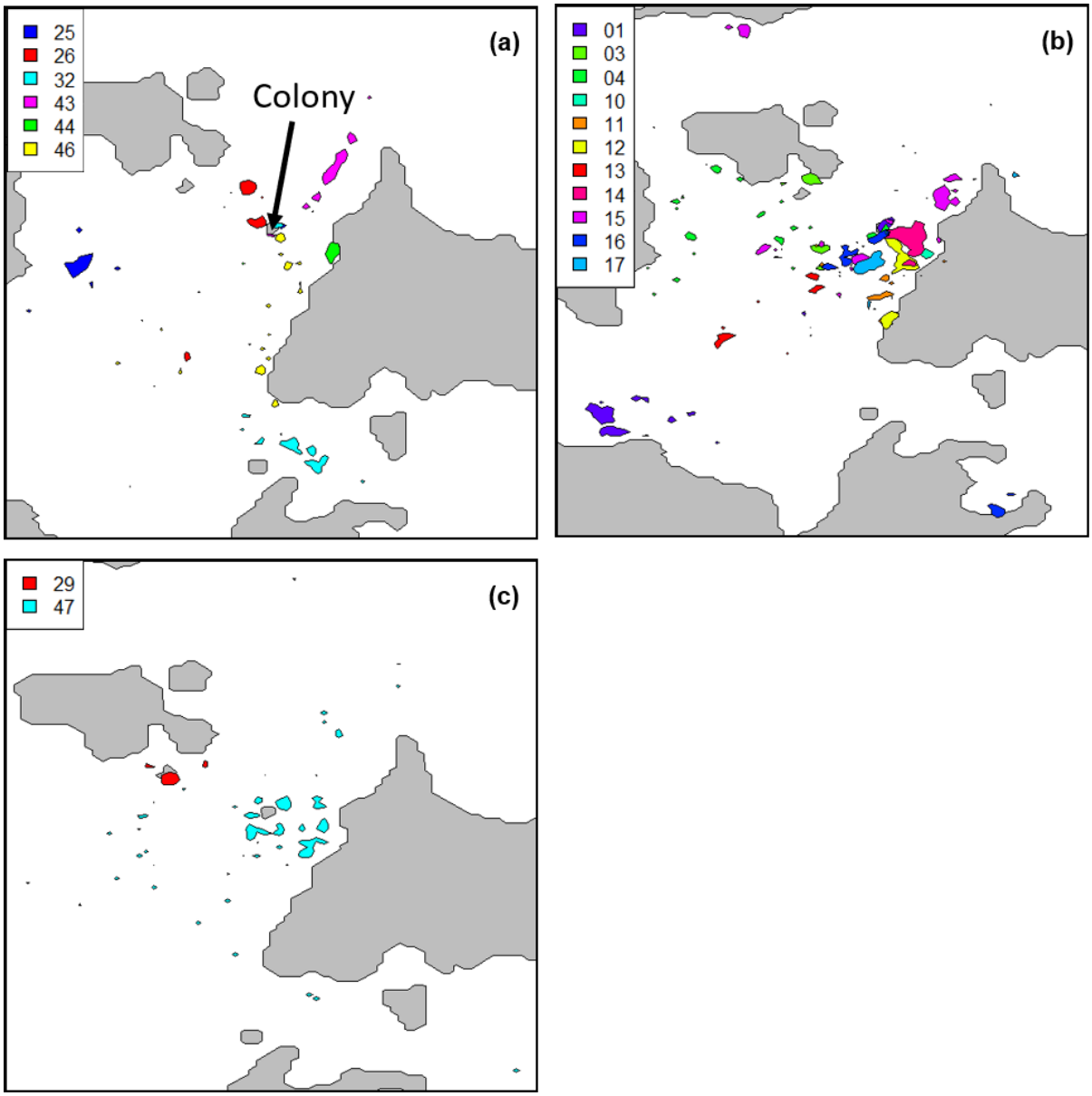


Figure 1: Raw GPS locations of (a) adult black guillemots tracked in 2013 n=6 and (b) 2014 n=11 and (c) immature black guillemots tracked in 2013 n=2. Colours indicate bird ID numbers. The triangle symbol indicates colony location.



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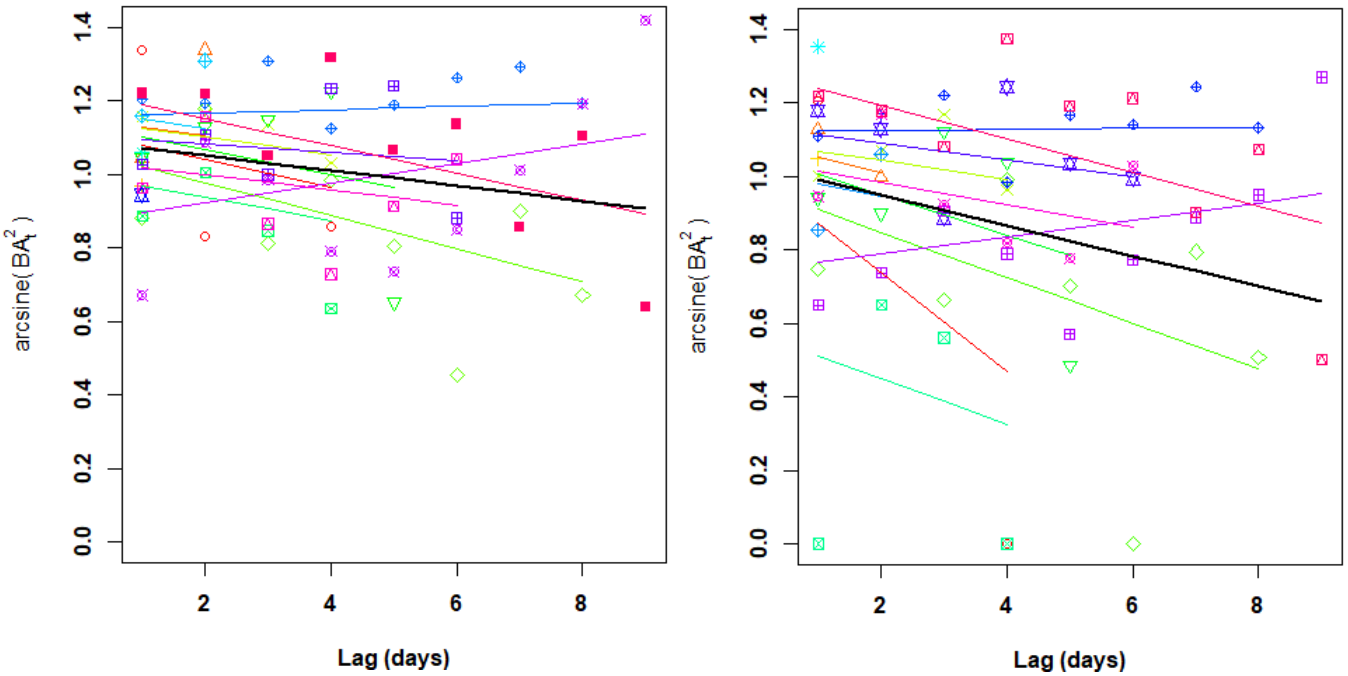
581 Figure 2: Utilisation distribution (50%) of adult black guillemots tracked in (a) 2013

582 n=6 and (b) 2014 n=11 and (c) immature black guillemots tracked in 2013 n=2.

583 Colours indicate bird ID numbers. The triangle symbol indicates colony location.



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586 Figure 3. Variation in individual foraging site fidelity of black guillemots over time (left
587 panel, all locations; right panel, putative foraging locations only). BA_t is the similarity
588 between the utilisation distribution of each individual on day 2 of tracking to that *t*
589 days later. Colours and symbols correspond to different individuals (n = 15) and the
590 black line is the predicted population-level response. Coloured lines are fitted curves
591 based on model coefficients for each individual.

592

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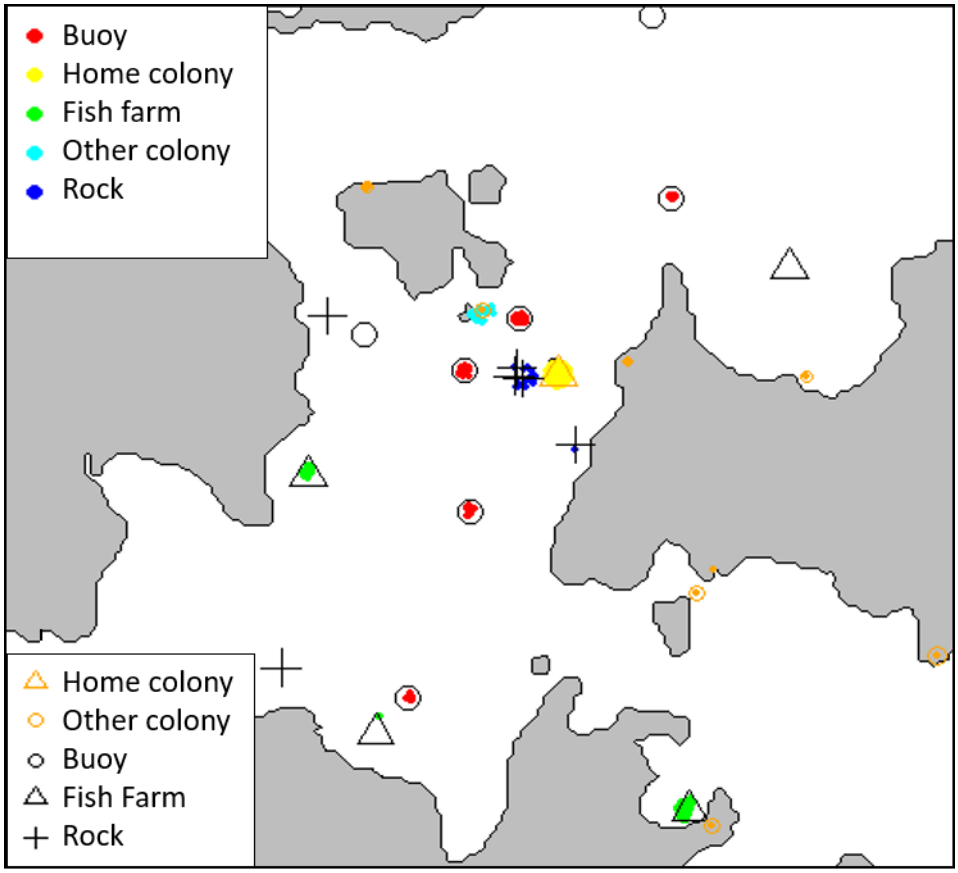


Figure 4: Potential roosting features (symbols) and tracking points where birds recorded used this feature (coloured by feature type).

Electronic supplements

Table S1: Width of buffers around fixed marine features used to classify behaviour at bird tracking locations. Behaviour was classified as at rest in/on a feature if location was within that feature's buffer and the speed was <0.5 m/s. All remaining locations were classified as 'at sea or in flight'

Feature	Name	Latitude	Longitude	Buffer[1] (m)
Study colony	Grassholm	59.0604	-2.9349	200
Other colony	Head of Holland	58.9924	-2.8928	200
	Gairsay 1	59.0888	-2.9878	200
	Gairsay 2	59.0888	-2.9878	200
	Helliar Holm	59.0274	-2.8972	200
	Holm of Boray	59.0701	-2.9559	200
	Shapinsay 1	59.0600	-2.8667	200
	Shapinsay 2	59.0623	-2.9156	200
	Shapinsay 3	59.0311	-2.8921	200
	Shapinsay 4	59.0180	-2.8308	200
	Shapinsay 5	59.0540	-2.8142	200
	Shapinsay 6	59.0883	-2.7993	200
Navigation buoy	Scargun Shoal	59.0115	-2.9765	100
	Linga Skerry	59.0398	-2.9594	100
	Seal Skerry	59.0663	-2.9881	100
	Skertours	59.0688	-2.9453	100
	Galt Ness	59.0868	-2.9035	100
	Wyre Skerries	59.1143	-3.0321	100
	Point of the Graand	59.1144	-2.9086	100
	Boray Skerries	59.0610	-2.9608	100
Fish farm[2]	Tor Ness	59.0452	-3.0041	200
	Veantrow Bay	59.0766	-2.8712	200
	Bay of Meil	58.9948	-2.8991	200
	Ramberry	59.0064	-2.9855	300
Isolated rock[2]	Skerry of Vasa	59.0499	-2.9302	100
	Holm of Rendall	59.0693	-2.9988	100
	Taing Skerry 1	59.0598	-2.9447	200
	Taing Skerry 2	59.0615	-2.9464	100
	Taing Skerry 3	59.0603	-2.9472	100
	Quanterne	59.0163	-3.0116	100

1. Measured from centre of feature.

2. Buffer size dependent on size of feature.

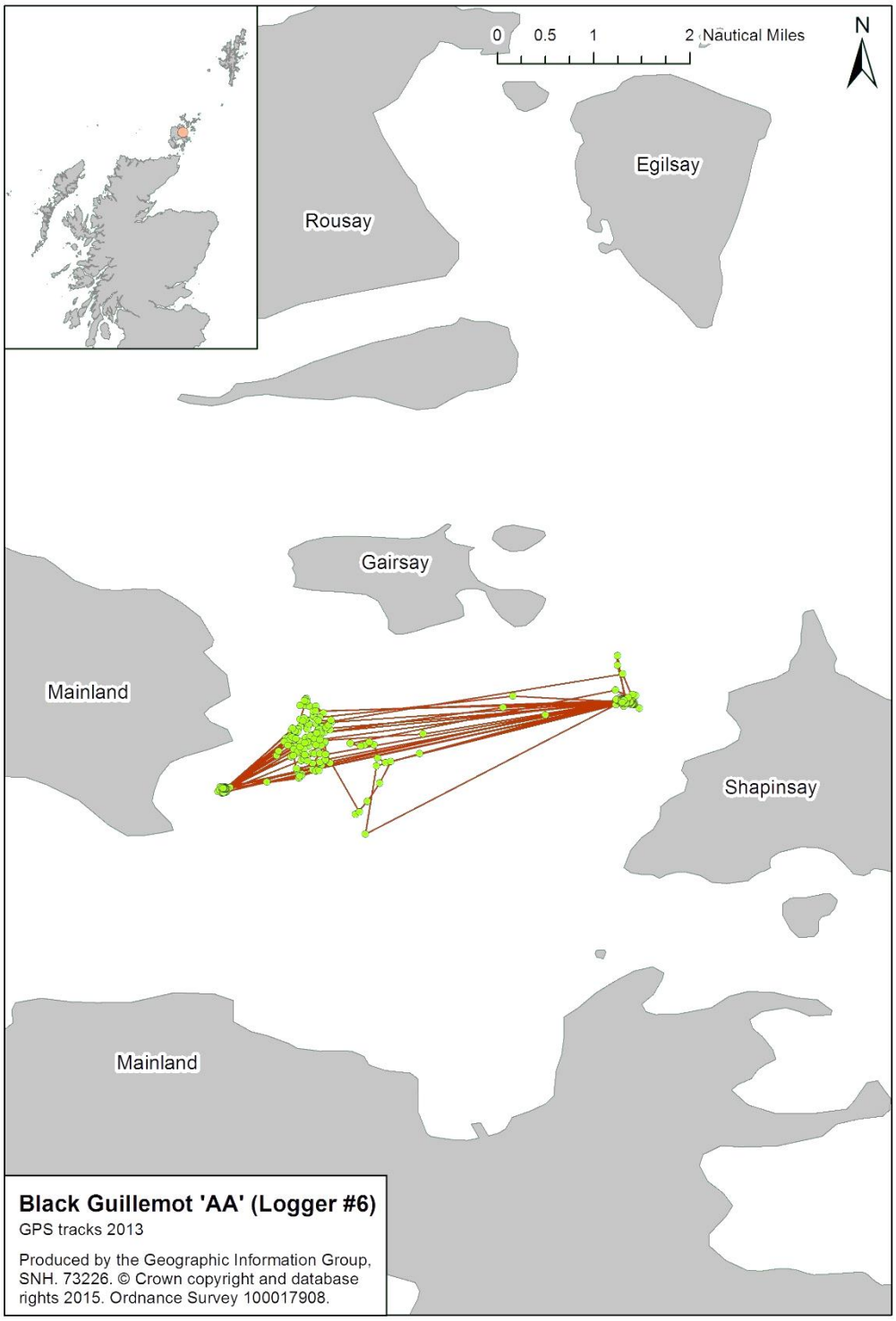
606 Table S2: One-way ANOVA showing differences between levels of IFSF (BA scores)
607 of immature (n=13 bird*day) and adult (n=76 bird*day) black guillemots at each of 11
608 scales from 100m to 5.7km. (df 1, 87).

609

Scale (km)	F	P
0.1	3.25	0.075
0.15	8.67	0.004
0.225	11.70	0.001
0.338	17.67	<0.001
0.506	15.48	<0.001
0.759	16.83	<0.001
1.139	15.31	<0.001
1.709	14.57	<0.001
2.563	33.55	<0.001
3.844	13.75	<0.001
5.767	22.72	<0.001

610

611 Figure S1: Individual birds tracked



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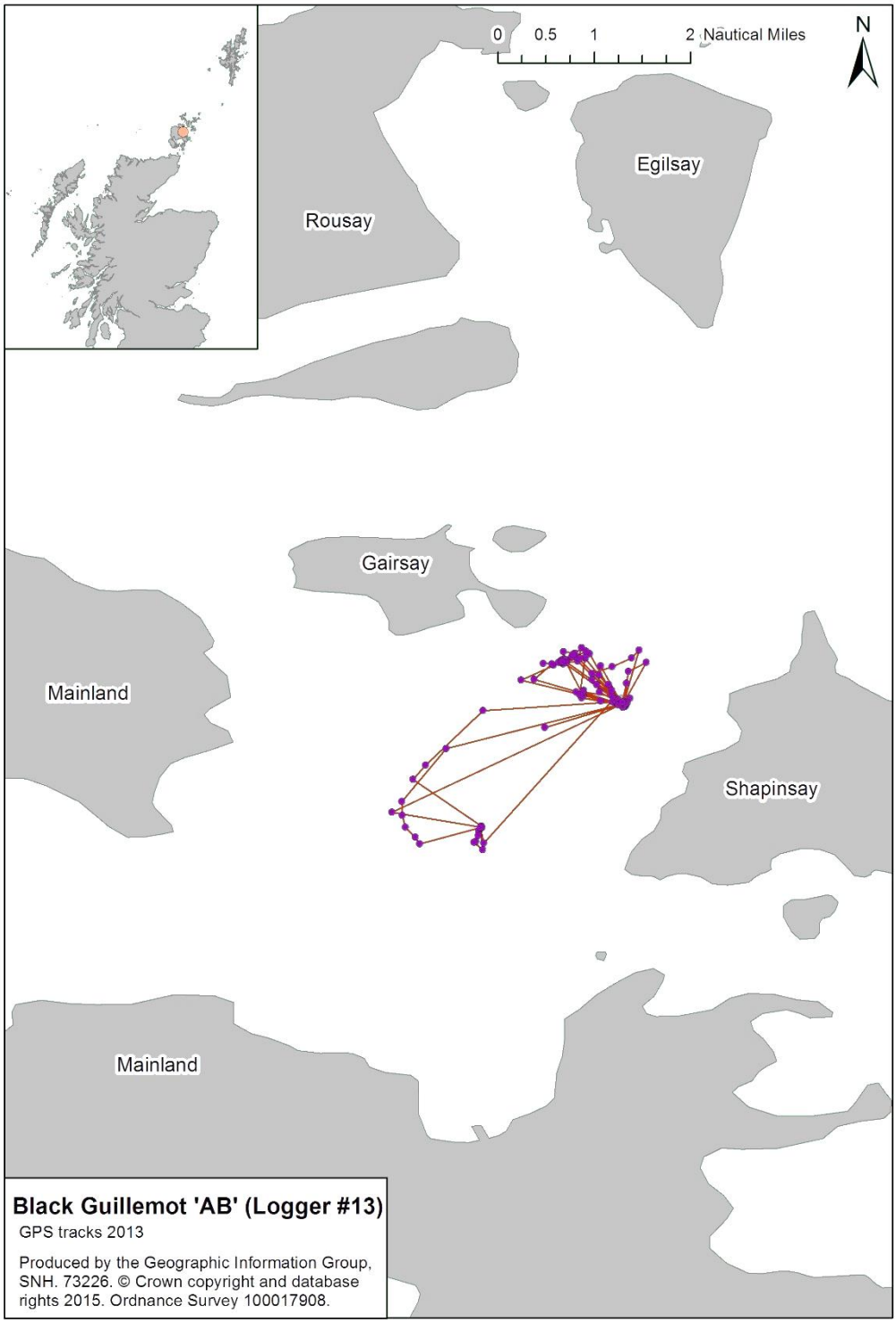
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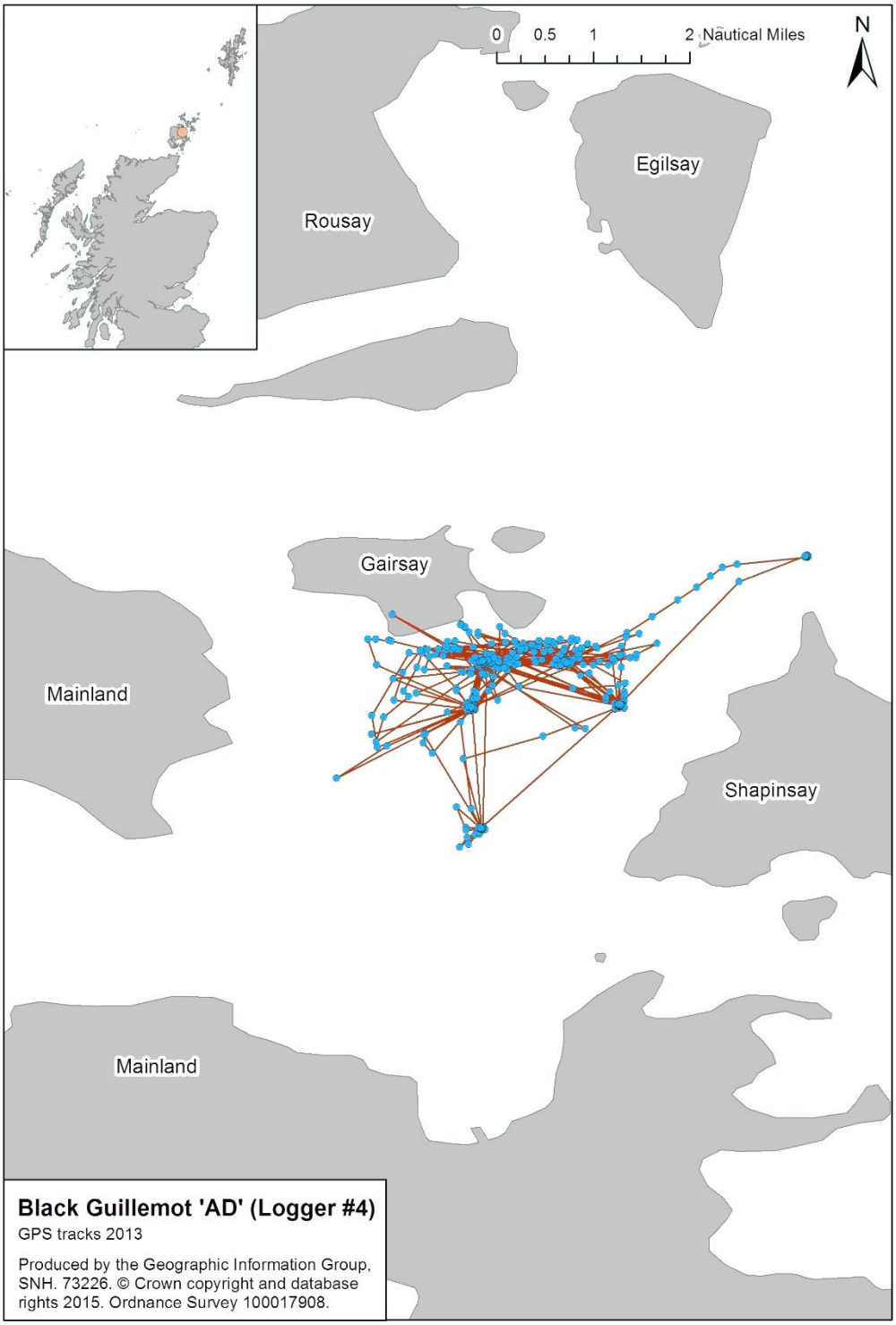
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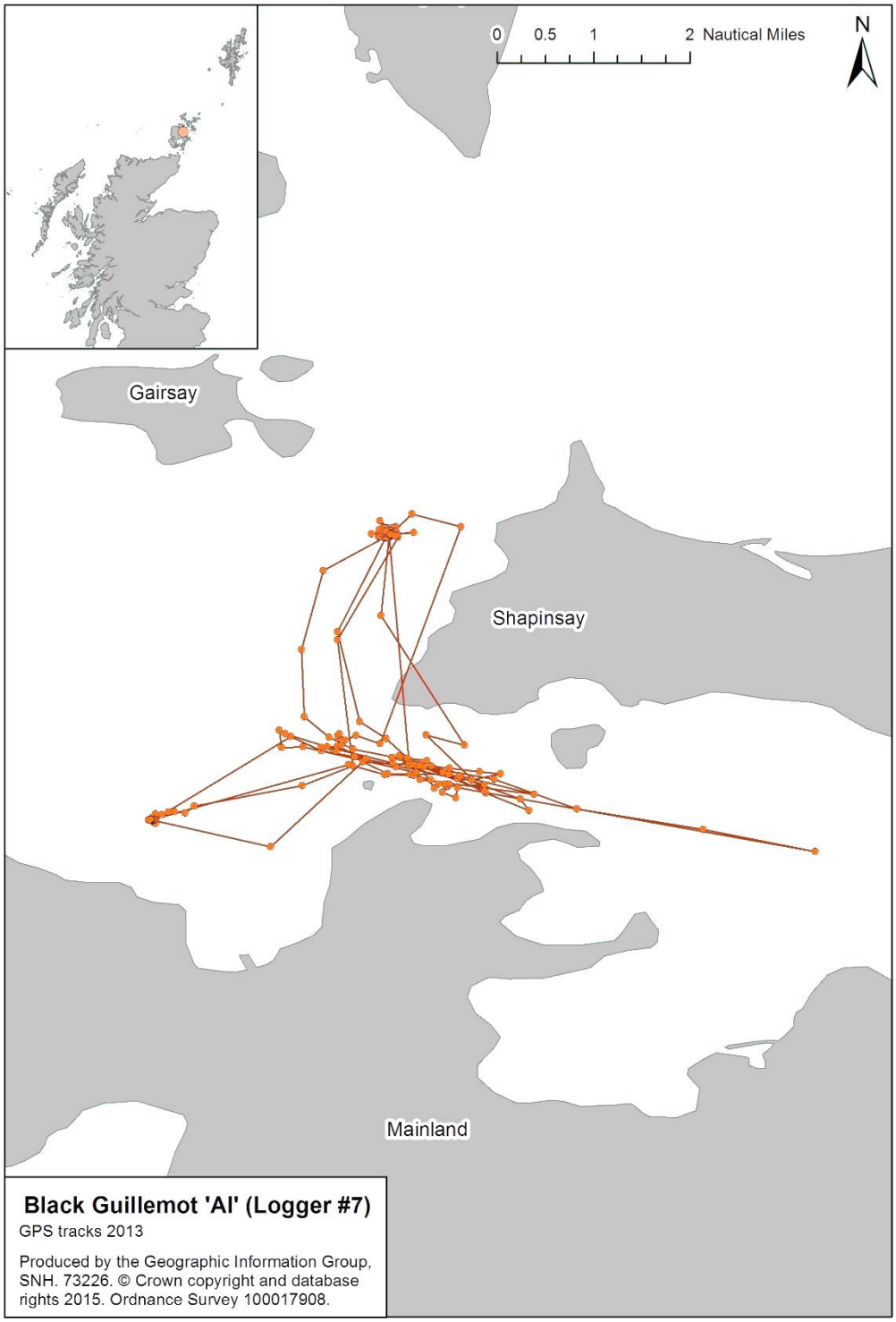
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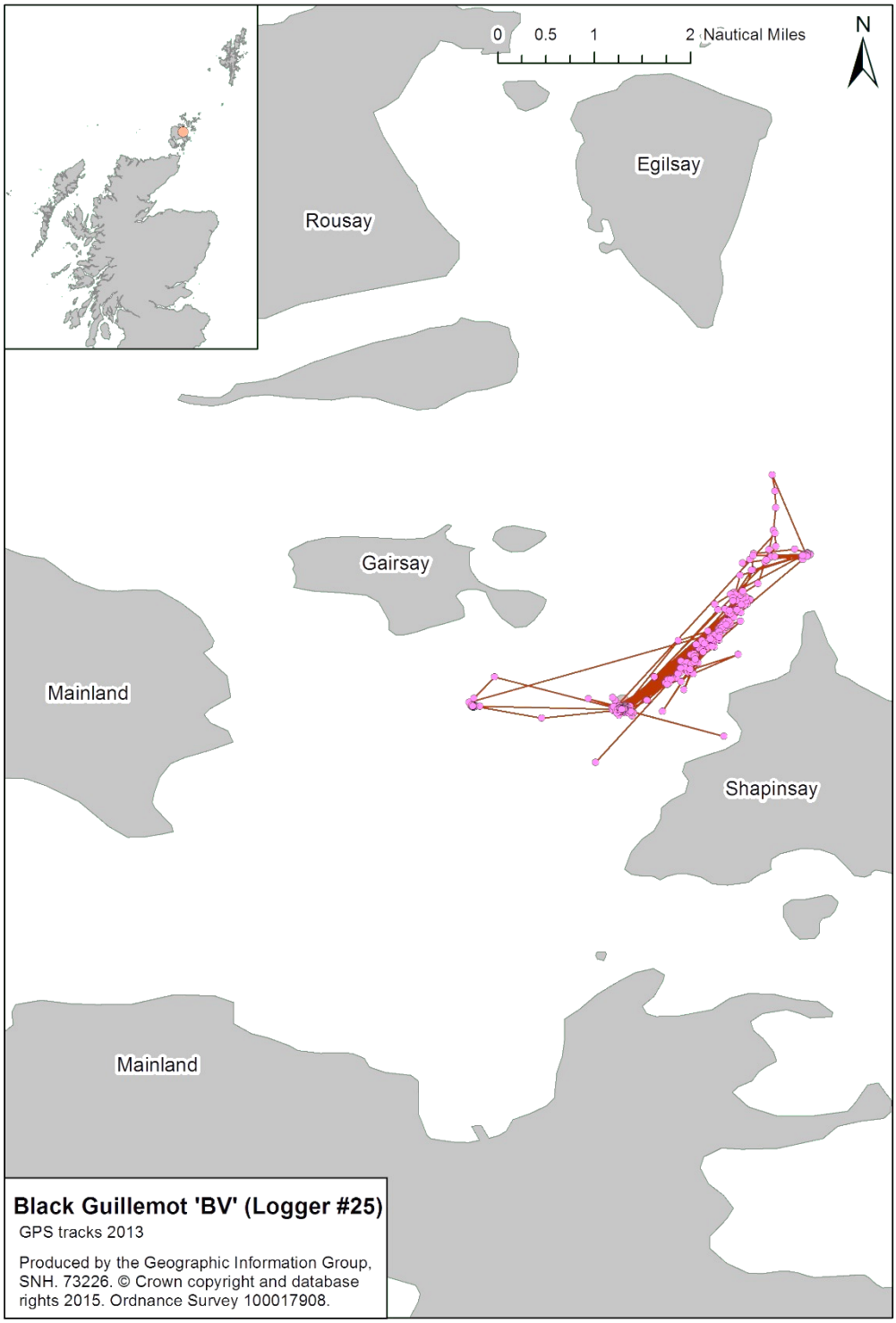
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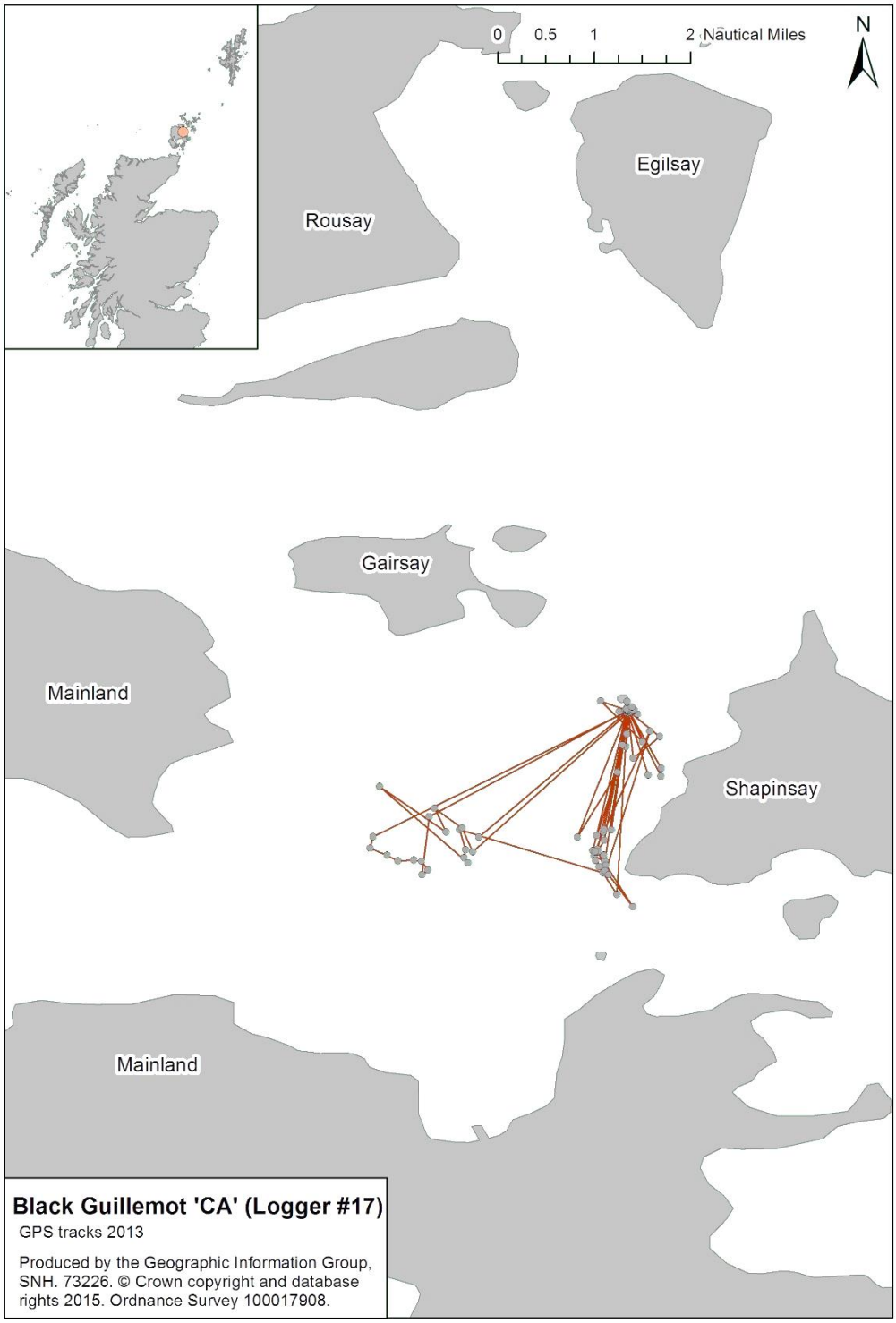
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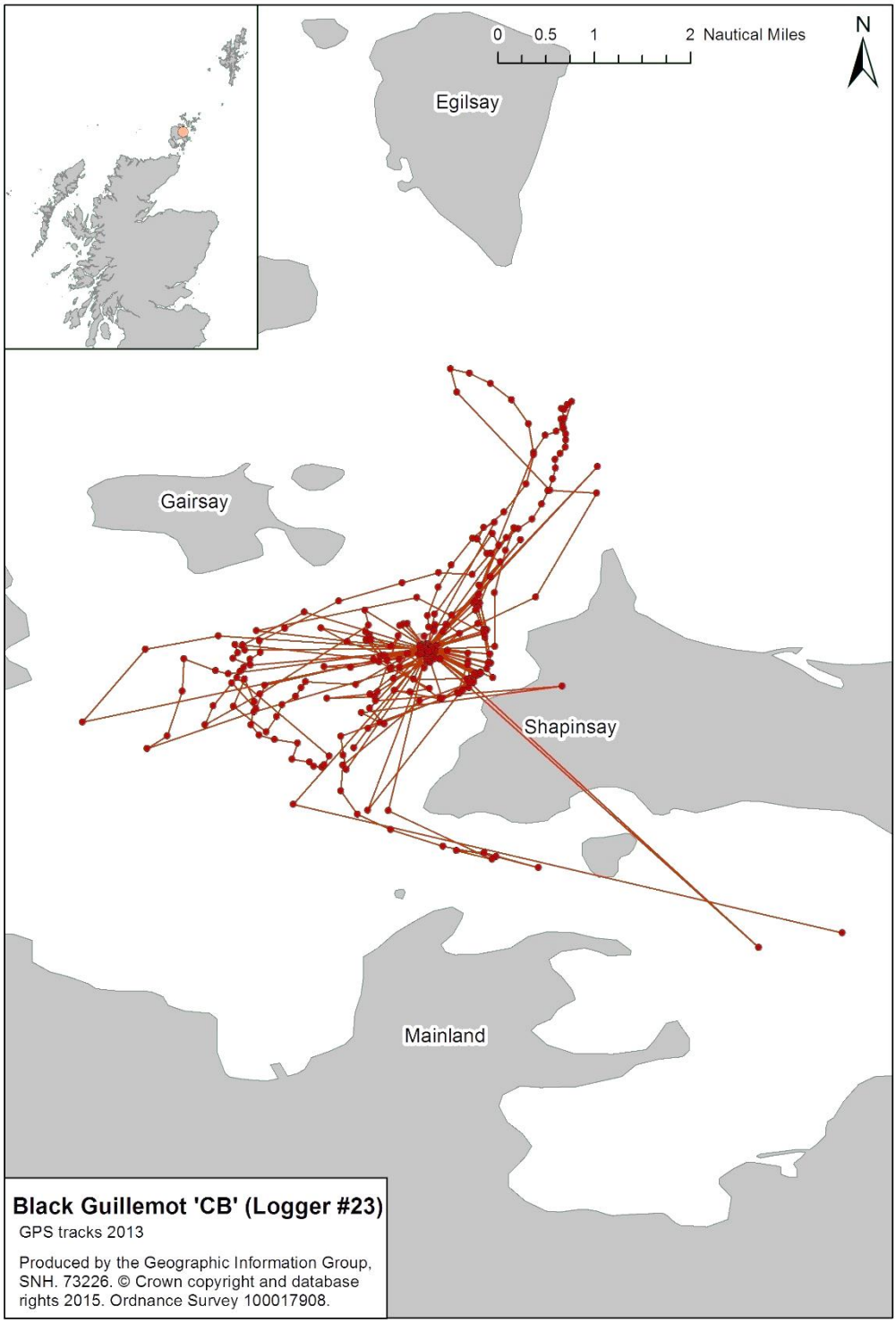
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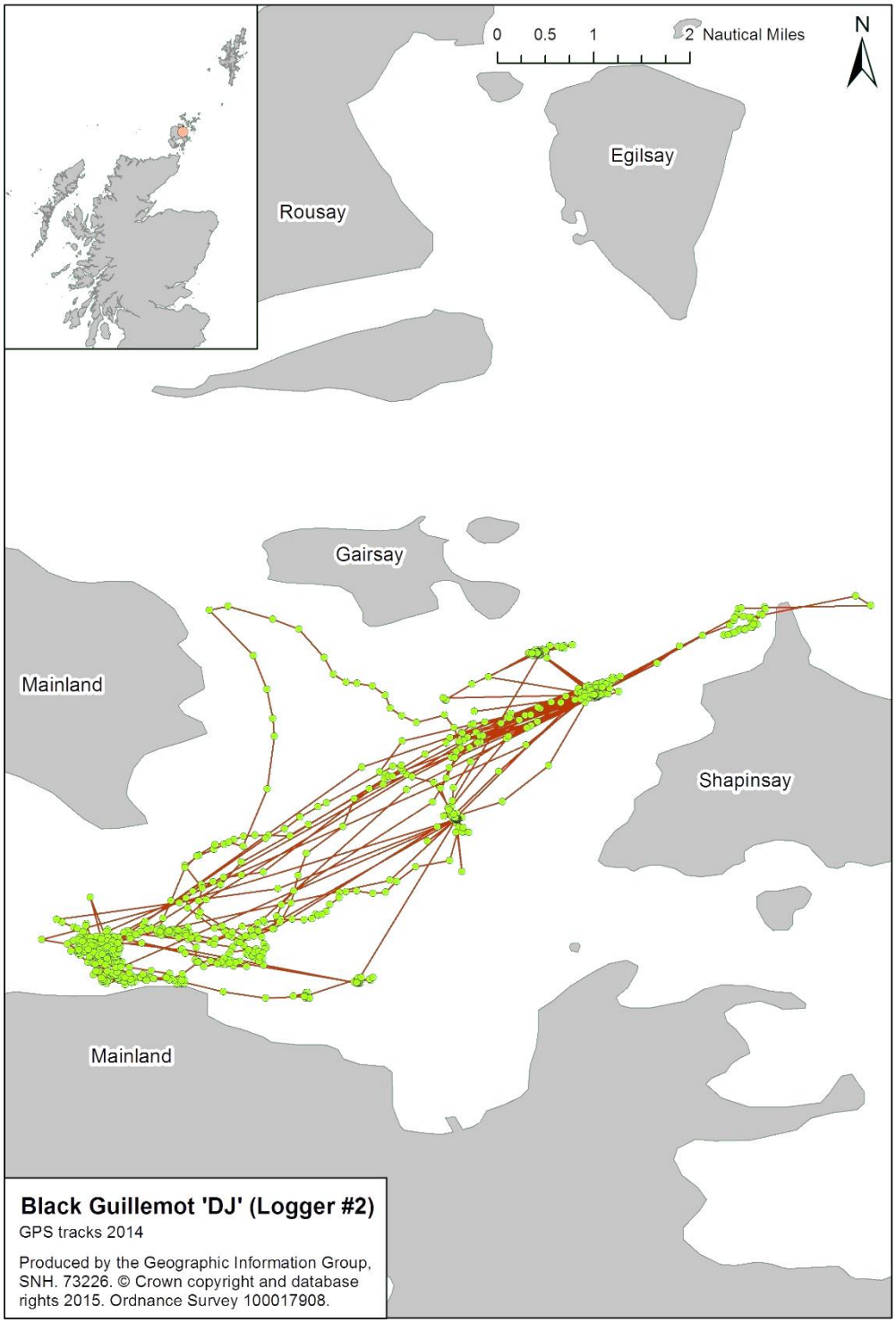

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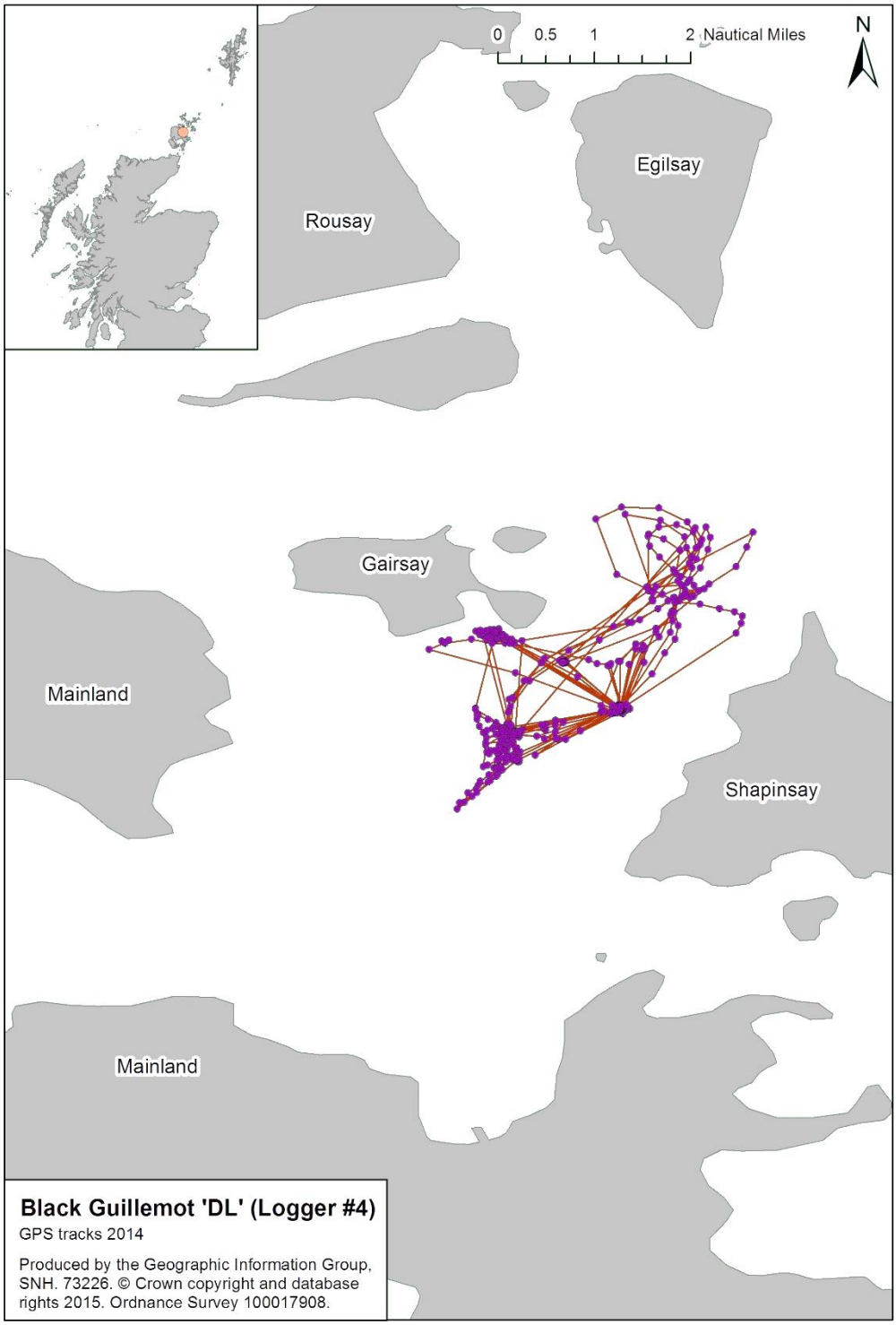
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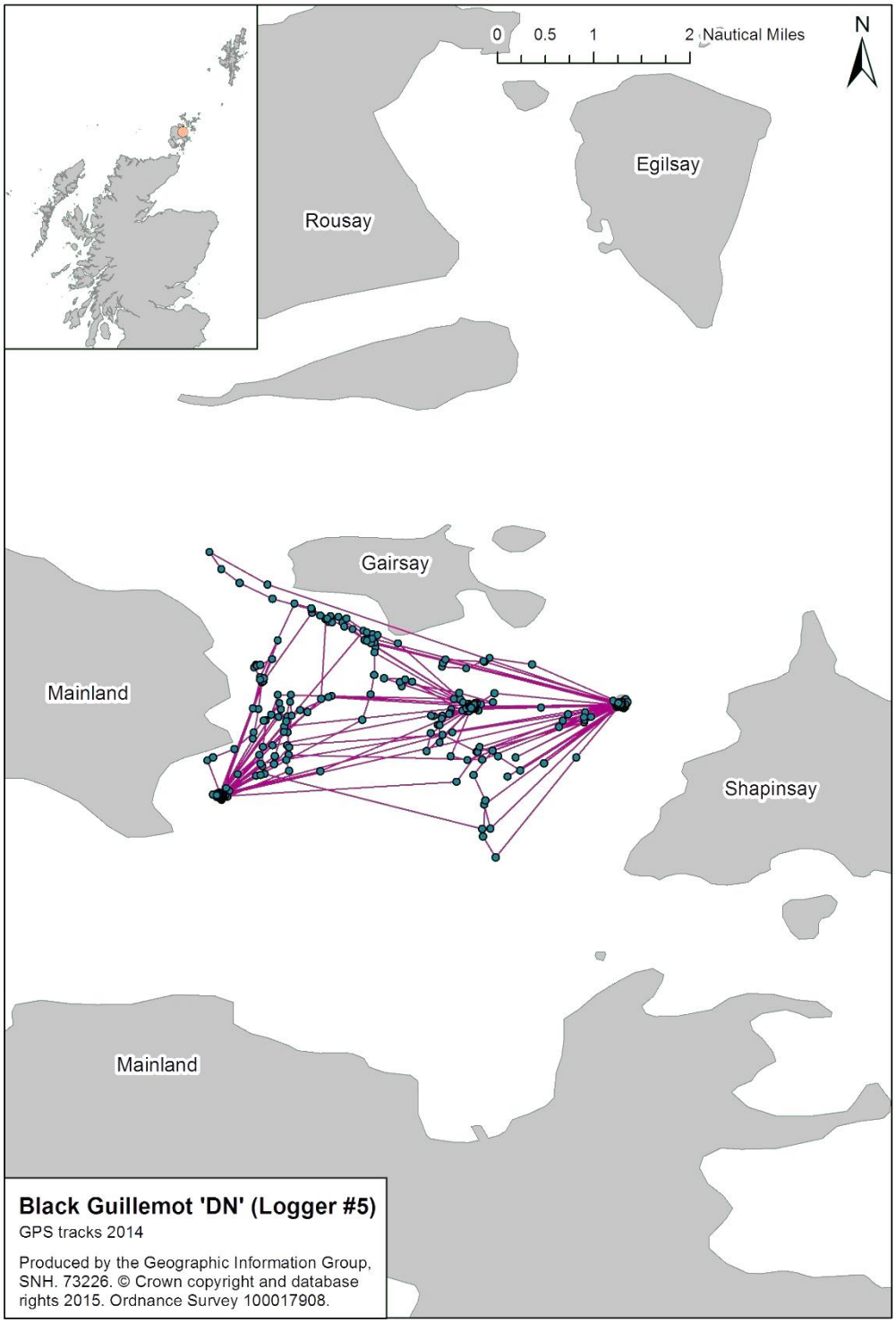
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GPS tracks 2014
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GPS tracks 2014
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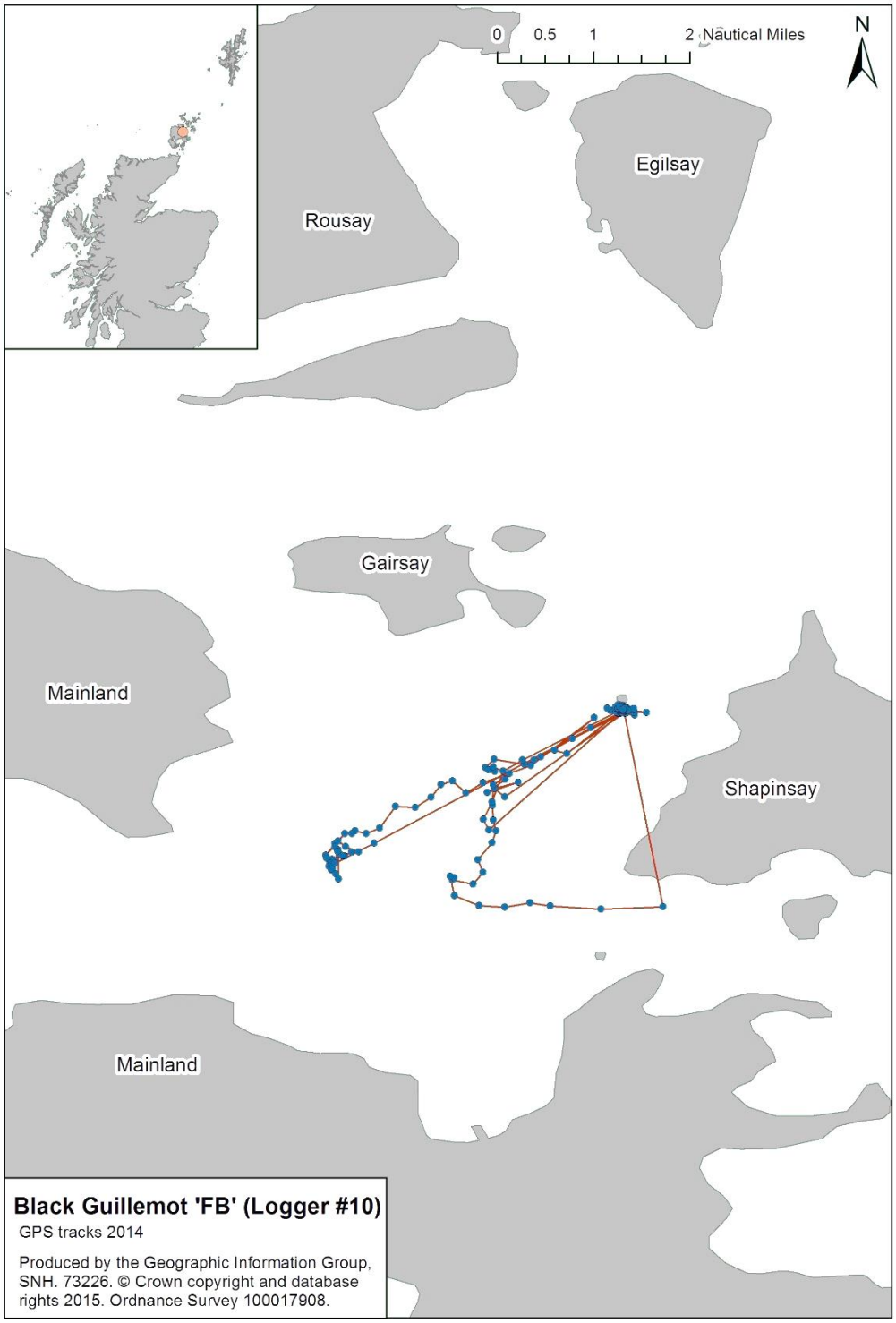
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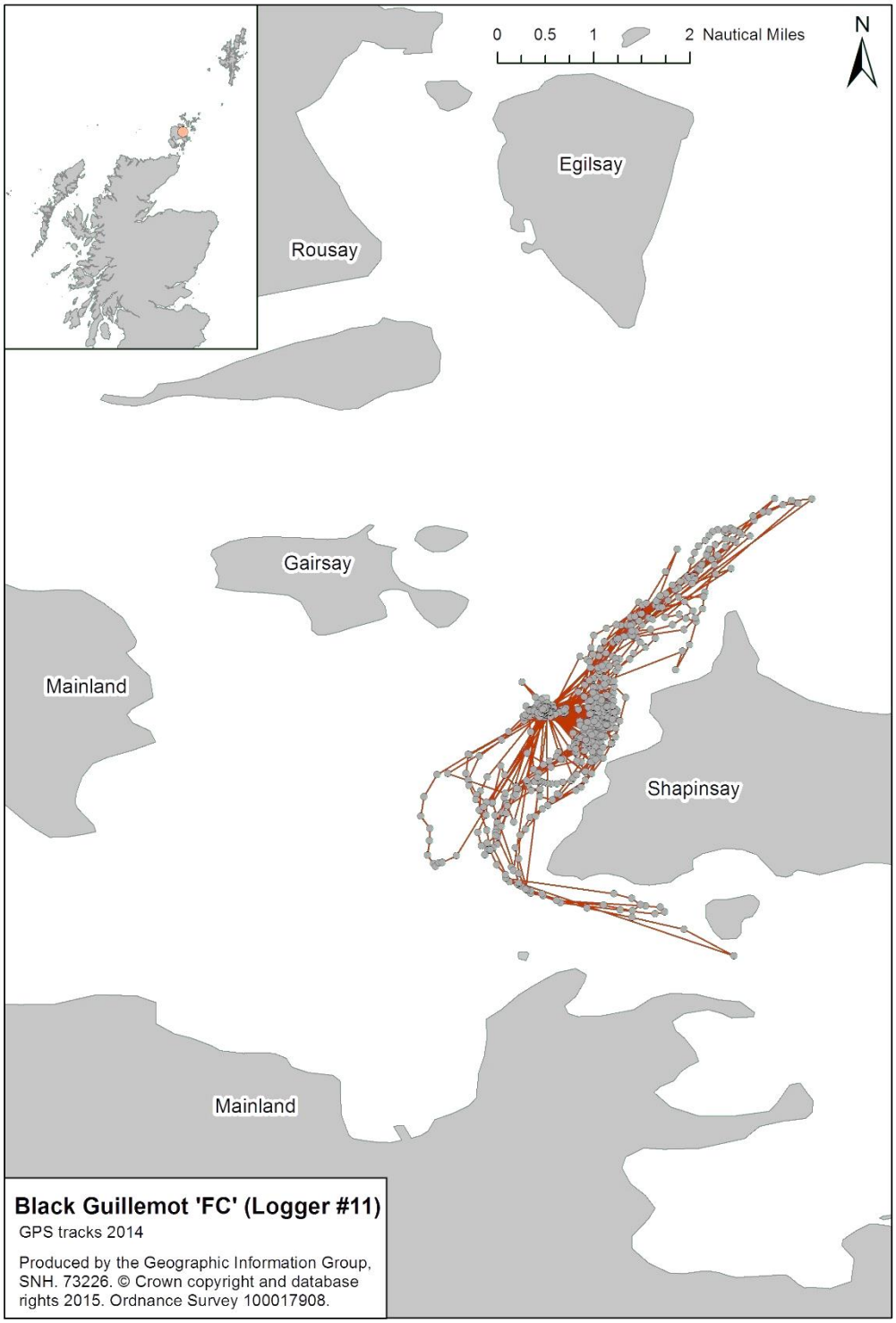
0 0.5 1 2 Nautical Miles
N
Egilsay
Rousay
Gairsay
Mainland
Shapinsay
Mainland
Black Guillemot 'FC' (Logger #11)
GPS tracks 2014
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0
0.5
1
2 Nautical Miles
N
Rousay
Egilsay
Gairsay
Mainland
Shapinsay
Mainland
Black Guillemot 'FD' (Logger #12)
GPS tracks 2014
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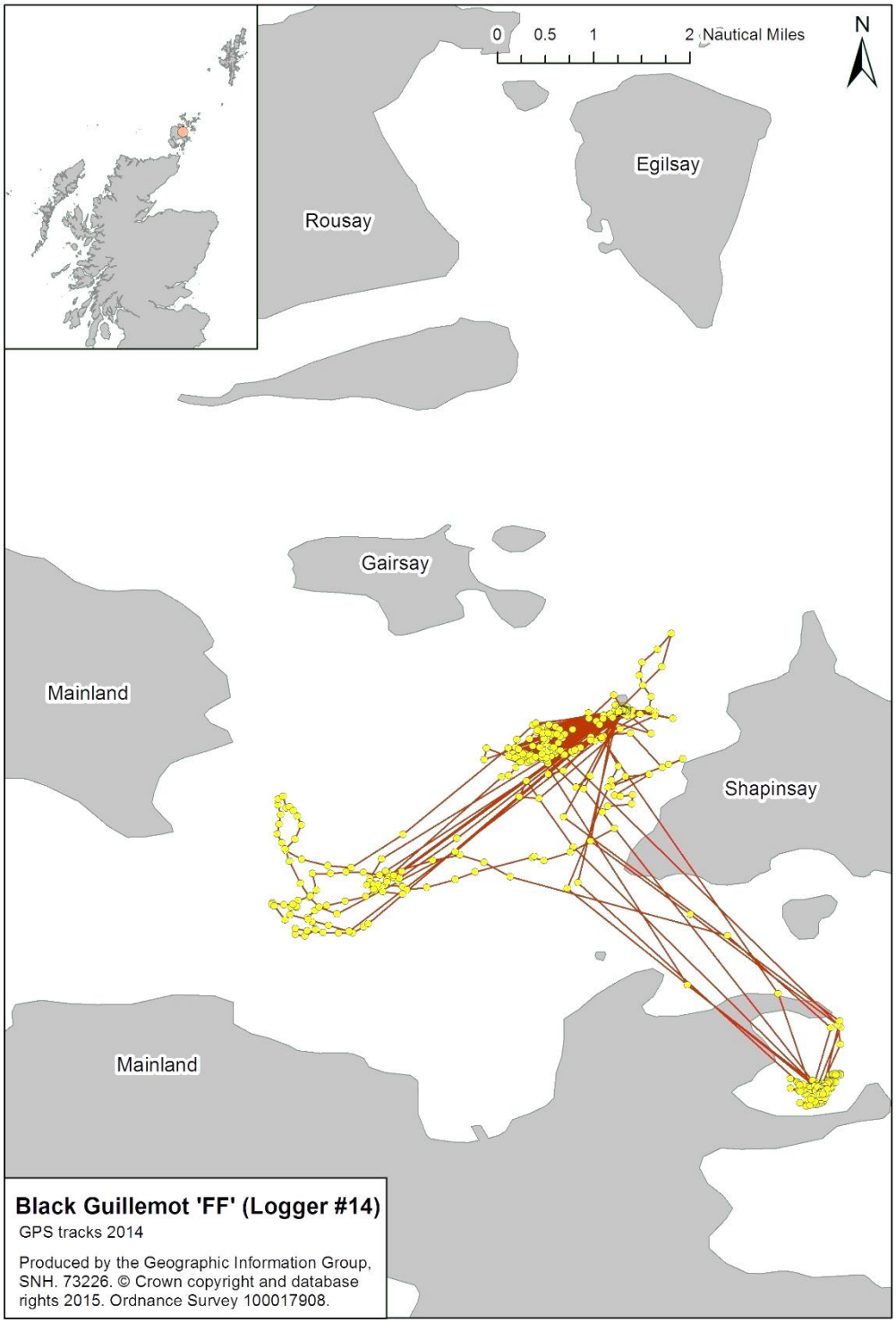
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0.5
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2 Nautical Miles
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Egilsay
Gairsay
Mainland
Shapinsay
Mainland
Black Guillemot 'FF' (Logger #14)
GPS tracks 2014
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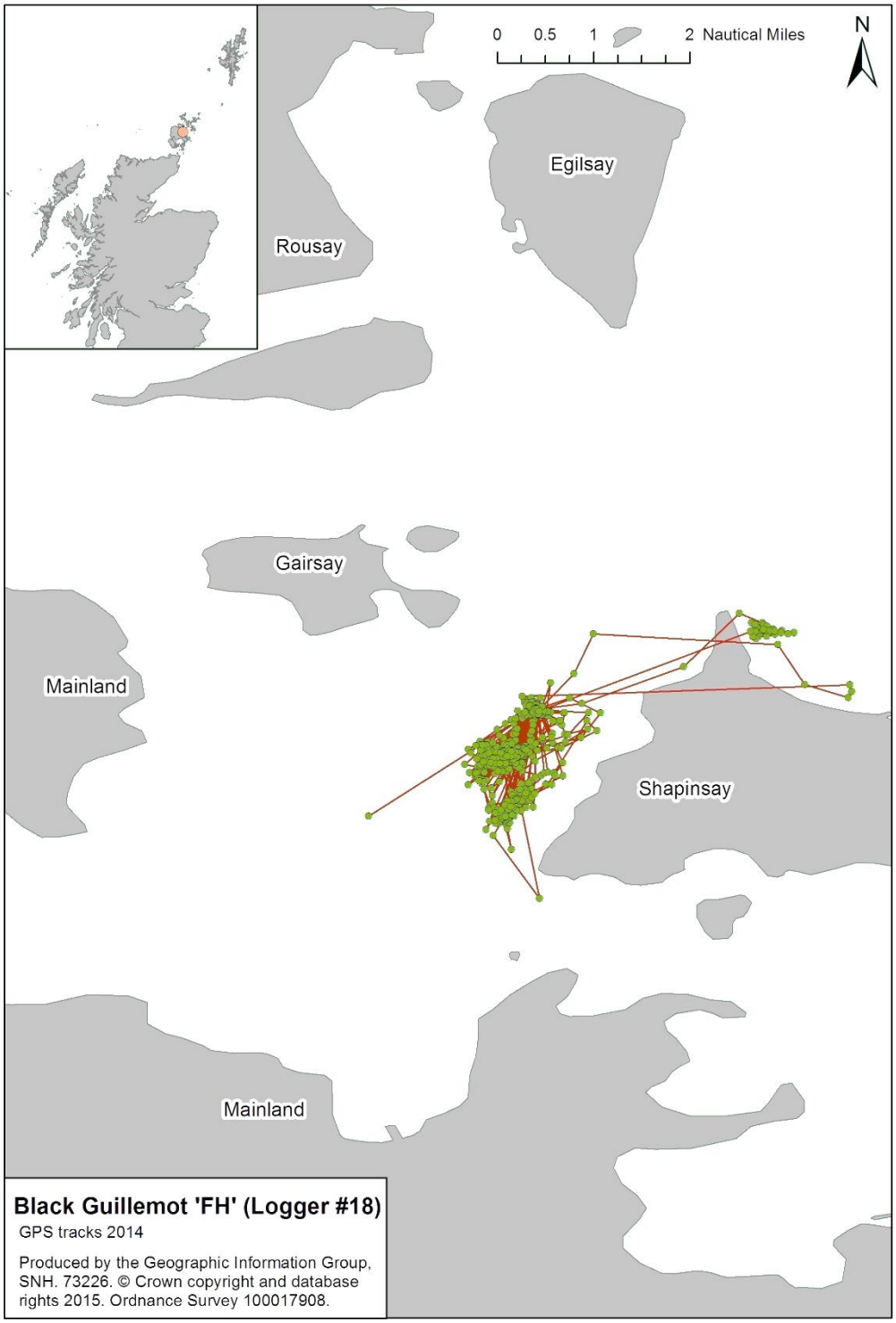
0 0.5 1 2 Nautical Miles
N
Egilsay
Rousay
Gairsay
Mainland
Shapinsay
Mainland
Black Guillemot 'FH' (Logger #18)
GPS tracks 2014
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Figure S2: Foraging trip durations and maximum distance from the colony from 19 black guillemots tracked over 2 years. Red line indicates the median value.

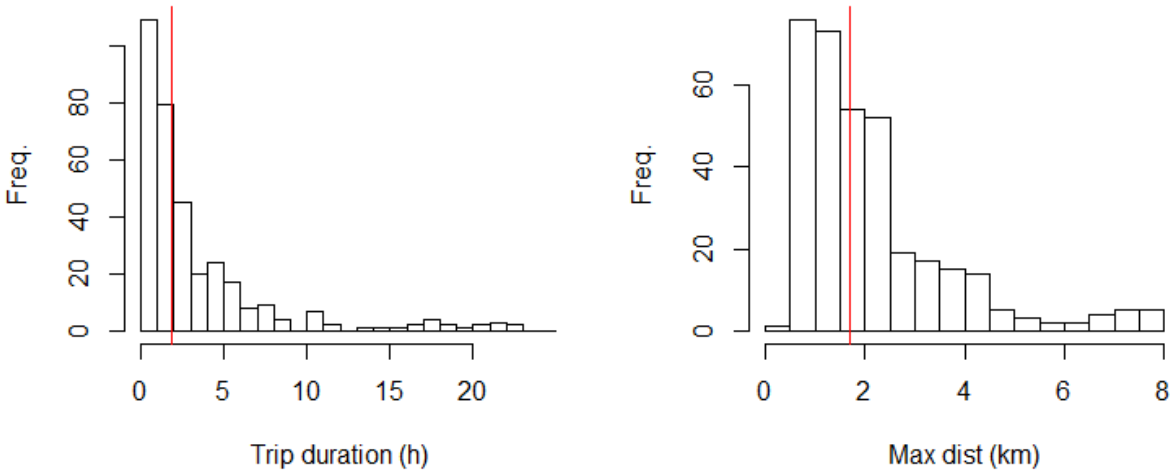
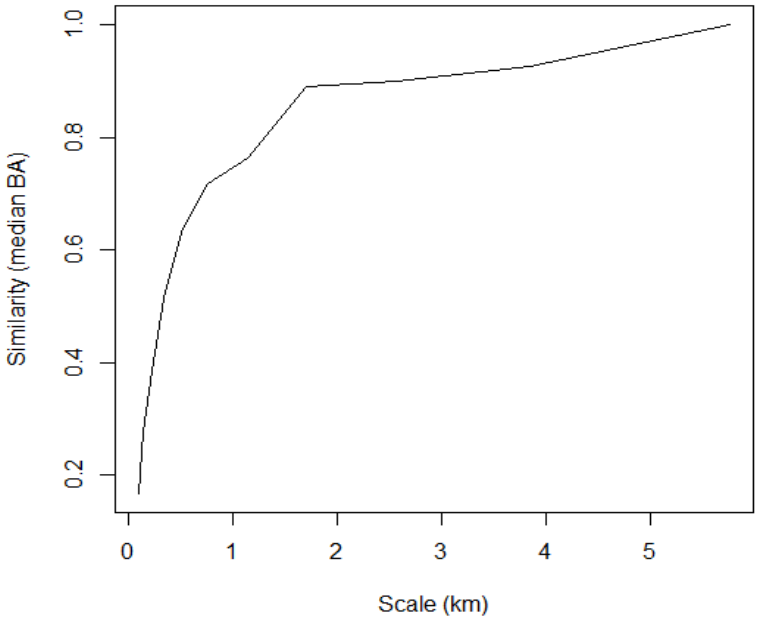
Figure S3. Variation in individual foraging site fidelity of black guillemots with spatial scale. Population-level median of the similarity (BA) between the utilisation distributions of each individual on 2 randomly selected tracking days, calculated on grids of varying scales.