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Golden Eagle Populations, Movements, and Landscape Barriers: Insights from Scotland

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Abstract: GPS satellite tracking allows novel investigations of how golden eagles *Aquila chrysaetos* use the landscape at several scales and at different life history stages, including research on geographical barriers which may prevent or limit range expansion or create population/sub-population isolation. If there are significant barriers to golden eagle movements, there could be demographic and genetic consequences. Genetic studies have led investigations on the identification of sub-species, populations, and sub-populations but should be conjoined with demographic studies and dispersal movements to understand fully such designations and their geographic delimitation. Scottish eagles are genetically differentiated from continental European birds, with thousands of years of separation creating a distinct population, though without sub-species assignation. They present unique research opportunities to examine barriers to movements illustrated by satellite tracking under Scotland's highly variable geography. We primarily examined two features, using more than seven million dispersal records from satellite tags fitted to 152 nestlings. The first was the presence of unsuitable terrestrial habitat. We found few movements across a region of largely unsuitable lowland habitat between upland regions substantially generated by geological features over 70 km apart (Highland Boundary Fault and Southern Uplands Fault). This was expected from the Golden Eagle Topography model, and presumed isolation was the premise for an ongoing reinforcement project in the south of Scotland, translocating eagles from the north (South Scotland Golden Eagle Project: SSGEP). Second was that larger expanses of water can be a barrier. We found that, for a northwestern archipelago (Outer Hebrides), isolated by ≥24 km of sea (and with prior assignation of genetical and historical separation), there were no tagged bird movements with the Inner Hebrides and/or the Highlands mainland (the main sub-population), confirming their characterisation as a second sub-population. Results on the willingness of eagles to cross open sea or sea lochs (fjords) elsewhere in Scotland were consistent on distance. While apparently weaker than the Outer Hebrides in terms of separation, the designation of a third sub-population in the south of Scotland seems appropriate. Our results validate the SSGEP, as we also observed no movement of birds across closer sea crossings from abundant Highland sources to the Southern Uplands. Based on telemetric results, we also identified where any re-colonisation of England, due to the SSGEP, is most likely to occur. We emphasise, nevertheless, that our study's records during dispersal will be greater than the natal dispersal distances (NDDs), when birds settle to breed after dispersal, and NDDs are the better shorter arbiter for connectivity.

Keywords: geographical barriers; *Aquila chrysaetos*; movements; satellite telemetry; population; natal dispersal; juvenile dispersal; raptor

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1. Introduction

The advent of GPS satellite tagging combined with technological advancements and the increasing deployment of tags has progressed knowledge of many birds' biology [1]. Satellite tracking allows for novel investigations of how golden eagles *Aquila chrysaetos* use the landscape at a range of scales and during different life history stages (e.g., [2–7]). This can include research on geographical barriers that may prevent or limit range expansion or create population/sub-population isolation. If there are significant barriers to golden eagle movements, there could be demographic and genetic consequences [6,8–11] with applied relevance for conservation.

There are large-scale examples of such geographical barriers, such that insular isolation has led to sub-species classification for Japanese birds (*A. c. japonica*) [12,13]. In Europe, birds around the Mediterranean Sea are classed as a different sub-species (*A. c. homeyeri*) to those further north, classed as the nominate subspecies [9,10], and North American birds (*A. c. canadensis*) are classed as one of six recognised sub-species, along with additional Asian sub-species [14–16].

These sub-species classifications are associated with obvious geographical barriers such as continents, oceans, extensive seawater, and/or large tracts of unsuitable terrestrial habitat. Such large-scale barriers have seldom been affirmed via satellite telemetric data [17]. This shortage of affirmation can be through a shortage/absence of telemetric data, or, when such data show a lack of movement connectivity at large-scale distances, they are not deemed to deserve commentary and/or they are implicitly obvious otherwise from genetic or taxonomic research. In the USA, assignations of populations and their distributions (including migratory birds) remain subject to further research but have received considerable illumination from satellite telemetry [17–19].

Related, though less obvious and rarely studied, however, are potential barriers to movement that may occur at finer scales and their geographical bases. Behind and beyond sub-species recognition, such considerations are essential to defining a "population" [20] or a "sub-population" [21] of golden eagles, which is fundamental in conservation efforts and their practical application [11,15,17,22,23]. Typically, these evaluations refer to genetics (e.g., [9–11,13,15]). Genetic studies have their limitations, however, and should be conjoined with demographic studies and dispersal movements to understand fully population and sub-population structures and their geographic delimitation [21].

Beyond recording the natal dispersal distance (NDD) and the distances moved during natal/juvenile dispersal (juvenile dispersal distance, JDD) (e.g., [6,23–25]), this subject has seldom been considered explicitly for golden eagles [17,22]. Despite the species' widespread Holarctic distribution [16], the global opportunities for contemporary research on landscape barriers at finer scales may be limited, or seldom explored, when most focus has been intra- or inter-continental [9,10,15,17].

Scotland hosts well over a thousand golden eagles [26] that were once more widespread across other parts of Great Britain (England and Wales) and the island of Ireland [11,16,27,28]. These birds have been isolated from mainland Europe for thousands of years but are not considered a separate sub-species, despite genetic differences [9–11,13]. Nonetheless, golden eagles in these islands on the northeastern fringe of the Atlantic Ocean clearly constitute a population [20], with Scotland currently hosting the substantial core.

Scottish eagles present unique research opportunities to examine possible finer-scale barriers via movements illustrated by satellite tracking, with consequential influence on demographic and genetic exchange and practical applications. There are at least two geographical features that may prevent or limit such exchange within the islands of Great Britain and Ireland, with Scotland providing an exemplar study area due to relatively high abundance and considerable research attention from numerous tagged eagles (e.g., [3,4,9,29,30]).

First, unsuitable terrestrial habitat may be a barrier. Scotland has a diverse geological landscape with seven major fault lines [31–34], although not all of them may be influential in affecting the movements and genetic exchange of golden eagles (Figure 1). The most obvious possible example is the separation between the Highlands and the Southern

Uplands, with the Lowlands (Midland Valley) as a prospective barrier based on geological boundary faults (Figure 1). Geology is intrinsically linked to topography, and topography is a critical component of golden eagle habitat preference and selection because of their adaptation to exploit anabatic and orographic winds, to provide vertical lift for most flight (e.g., [3,35–37]). When airspace is a critical habitat for many soaring birds [38], the Golden Eagle Topography (GET) model surrogates several topographic features for orographic wind lift and is a robust repeatable proxy for golden eagle habitat preference [3,29].

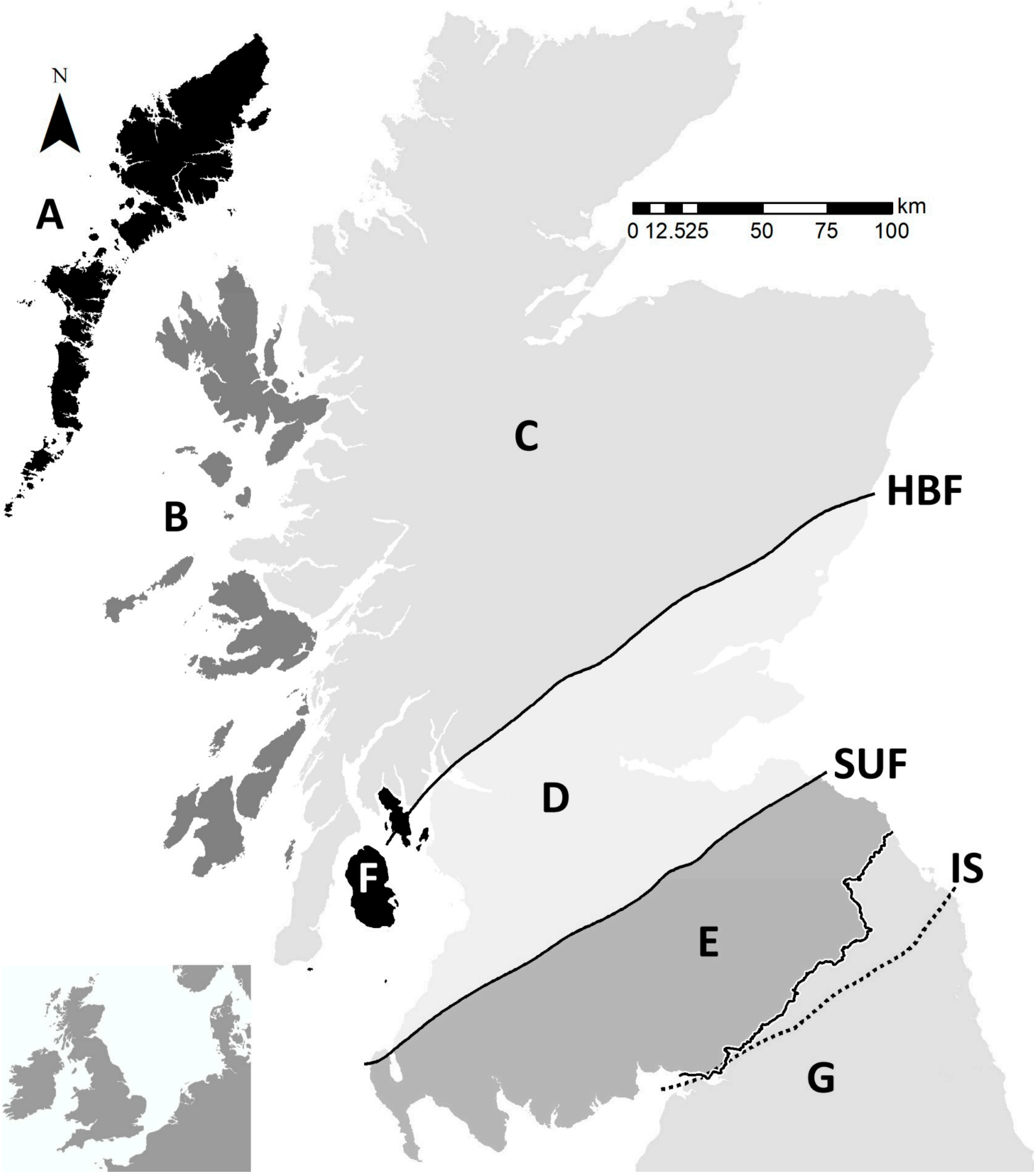

Figure 1. Regions of Scotland (unattributed black solid line shows the political boundary between Scotland and England): A Outer Hebrides, B Inner Hebrides, C Highlands, D Lowlands (Midland Valley), E Southern Uplands, F Clyde Islands, and G England. Also shown are selected geological fault lines: HBF = Highland Boundary Fault, SUF = Southern Uplands Fault, IS = Iapetus Suture (dotted line, where, once separated by a large ocean, "Scotland" and "England" were brought together by tectonic movements). The inset shows the location of the UK and the Republic of Ireland within western Europe. Contains Ordnance Survey data © Crown copyright and database right 2020.

Second, larger expanses of water can be a barrier to movement [35,36,39] and genetic exchange [12,13,15]. Globally, these seem obvious in several golden eagle sub-speciation examples. Within Scotland, genetic evidence indicates that birds on the Outer Hebrides (Western Isles) are largely separated from the rest of Scotland [8], confirming historical data [28,40], and, as such, they may effectively be a sub-population. The Outer Hebrides are on the northwestern edge of Scotland, facing the northeastern Atlantic Ocean, with at least 24 km of sea (the Minch) separating them from the Inner Hebrides, and the Scottish mainland further away (Figure 1). There are high densities of golden eagles in both the Outer and Inner Hebrides [26].

Scotland has over 900 islands [41,42] and numerous sea lochs (fjords), mostly in the west of the eagle population's distribution. This large geographical resource in Scotland, underlying the distribution of golden eagles, can allow for the examination, via telemetry data, of the extent of water that may be a barrier to movement.

Repeated national censuses from 1982/83 to 2015 [26,43–45] found that in some regions, away from persecution through the intensive management for shooting red grouse *Lagopus lagopus scotica* [30,46,47], the number of pairs in the Highlands and Islands had progressively risen, in western regions particularly. In parts of the Central Highlands this increasing trend has continued since the last national 2015 census [48].

Such trends were not evident in the Southern Uplands, however, with a stagnant potentially moribund group, and only four pairs identified in 2015 [26], in a region with recent prior evidence of persecution [46,49,50]. This small regional vulnerable persistence was against a backdrop suggesting scope for several more territorial pairs, with historical placename records indicating a possible 20–25 prior territories [28]. Adding more contemporary information, potentially 10–14 pairs were estimated [50] using several published sources (e.g., [28,51–53]), local knowledge (C. Rollie, pers. comm.), and novel estimates of suitable habitat distribution [50]. These estimates of suitable habitat distribution used a precursor of the GET model, subsequently expanded, and were confirmed as robust [3] and further verified [29].

Given the available evidence, the Scottish Government decided that, as natural expansion was apparently being thwarted, putatively by spatial isolation, largely the Lowlands (Midland Valley, Figure 1), active reinforcement efforts were needed from translocations [50,54] to secure a self-sustaining sub-population in the Southern Uplands. Following [50], this led to the South of Scotland Golden Eagle Project (SSGEP: https://www.goldeneaglessouthofscotland.co.uk/ (accessed on 12 December 2023)), a reinforcement project (2019–current) which has predominantly translocated nestlings from the northern and western Highlands to be hacked [55,56] from release sites in the Southern Uplands. There were too few birds in the Southern Uplands for genetic evaluation of differences [8], but, with further information from tagged birds, including the SSGEP's tagging efforts, the premised isolation of the Southern Uplands and the justification for the SSGEP can, retrospectively, be examined further.

We used extensive Scottish golden eagle satellite tracking data to examine whether two features of unsuitable habitat (terrestrial and/or seawater, see above) can act as barriers to movement and so may generate three sub-populations within the Scottish population (i.e., the Outer Hebrides, the Southern Uplands, and the more extensive Highlands, Inner Hebrides, and Clyde Islands: Figure 1). Within this overarching objective, three hypotheses were evaluated.

Our first hypothesis is that two major geological fault lines create habitat changes [57] sufficient to restrict movements between them. The Lowlands (Midland Valley), between the Highland Boundary and the Southern Uplands Faults (Figure 1), would act as a barrier to movements to and from the south of Scotland because, partially influenced by geology [50,57,58], the Lowlands have little contiguous preferred eagle habitat as defined by the GET model [3,29].

Our second hypothesis is that there is a limit to a water body's width (extent of seawater) that dispersing golden eagles will cross. We consider first the extent of seawater that eagles are prepared to cross nationally, and the seasonal distribution of such crossings. With this backdrop, we examine the specific expectation that the Outer Hebrides (Figure 1) are sufficiently isolated to make such crossings rare events, leading to the effective isolation of an Outer Hebrides sub-population [8].

Related, we also examine sea crossings between the Highlands, Clyde Islands to and from the Southern Uplands and the south of Scotland (Figure 1) as another potential source of connectivity between the Highlands and the Southern Uplands (and the wider south of Scotland), aside from a potential terrestrial habitat barrier (the Lowlands, see hypothesis 1 above).

Our third hypothesis is that the south of Scotland and the north of England are unlikely to experience sufficient movements from the northern and western Highlands to facilitate the establishment and growth of a viable breeding group, without external intervention (translocations). Related, we also examine the movements between the south of Scotland and the north of England (Figure 1) that may indicate geographically where any re-colonisation of England from Scotland may be more likely.

2. Methods

2.1. Study Area

Scotland covers c. 80,000 km^2 on the northwestern limit of Europe and hosts over 500 territorial golden eagle pairs occupying Scotland's uplands [26], which are also used by hundreds of non-territorial birds [3,30,47]. These uplands vary in geology, vegetation, topography, and climatic influences [47,57,58].

Climatically, situated on the northeastern edge of the Atlantic Ocean, the west of Scotland is subjected more to the North Atlantic Drift and is wetter and windier, with more equitable seasonal changes in weather and, hence, more oceanic. The east is drier, with greater seasonal change in weather and, climatically, more continental [16,47,57,58].

The contrasting oceanic/continental influences tend to produce upland vegetations that in the east are only found at higher altitude but may occur at sea level in the west. The preferred open habitats are dry or wet heathland and peatland dominated by heather *Calluna vulgaris* and relatives in the east, with graminoids, sedges, and deeper peatland more common in the west [57].

Irrespective of vegetation, airspace is a critical habitat for soaring birds like golden eagles [38] and topography generates much of this habitat by affecting the available wind resources for efficient movement. A combination of altitude, slope, and distance from ridges robustly surrogates for orographic wind energy availability and is highly influential in eagle movements and distribution (GET model: [3,29]).

2.2. Study Species and GET Predictions

The study population has been described above and, repeatedly, elsewhere (e.g., [4,16,47,59]), with historical details in [59].

GET model predictions can be assigned to two categories, $\leq$5 (GET 1 to 5) and $\geq$6 (GET 6 to 10), loosely described as poor and good golden eagle habitats [3,29]. GET predictions were assigned to every 50 $\times$ 50 m pixel in Scotland and northern England (Figure 2).

2.3. GPS Tagging and Data Treatments

Previous Scottish studies have described in detail the methods used to tag nestling golden eagles and the absence of discernible adverse effects (e.g., [3,30]). All the tags in our study were solar-charged transmitters, with most models manufactured by MTI (Microwave Telemetry Inc., Columbia, MD, USA) as 70 g GPS/Argos or GPS/GSM PTTs. The tags deployed in the Outer Hebrides included OrniTrack 50 g GPS/GSM models (Ornitela, Vilnius, Lithuania).

We used more than seven million GPS records from tags fitted to 152 nestlings that subsequently dispersed. Twenty-eight birds were tagged between 2007 and 2010, 54 between 2011 and 2015, 54 between 2016 and 2020, and a further 16 up until 2022. The sex ratio was approximately equal, with 63 females, 62 males, and 27 of unknown sex.

We excluded data prior to dispersal from the natal range [2] or records from translocated hacked nestlings before they made comparable movements away from the release site in the south of Scotland under the SSGEP; the hacking/release site was taken as the presumptive natal site [24,29,54]. Forty-seven of the dispersing birds settled on a territory, but here we used pre-settlement data only for birds during natal dispersal [4,5], also termed juvenile dispersal [2,60], or the transience phase [61].

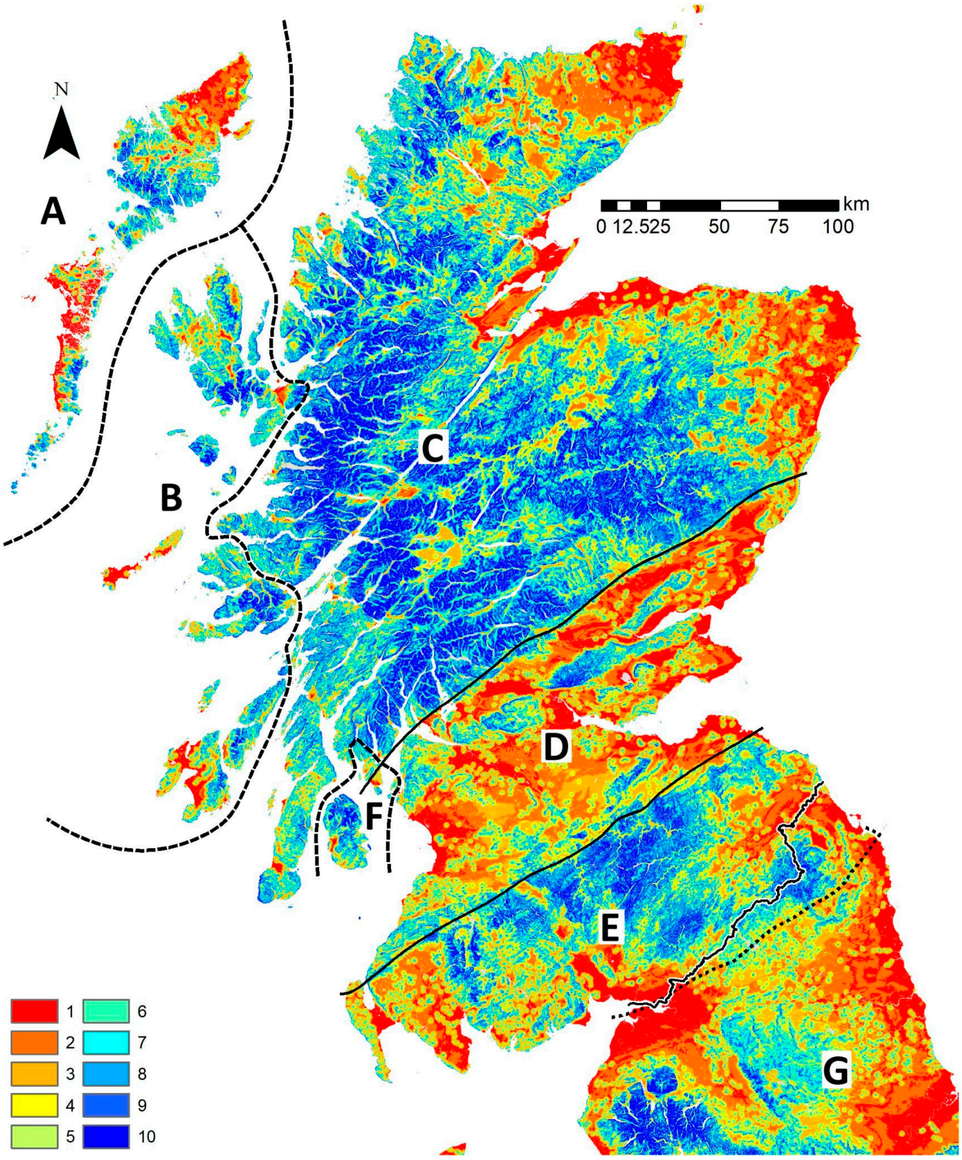

Figure 2. GET model predictions of terrestrial habitat suitability (1–10: ≥6 indicating preference) in Scotland and northern England. The backdrop shows seven regions (A–G), three geological boundary faults, and the political border between Scotland and England, described in Figure 1. Contains Ordnance Survey data © Crown copyright and database right 2020.

Of the study's 152 tags, 33 were deployed in the Outer Hebrides on Lewis (Region A: Figure 1), four in the Inner Hebrides (Region B: Figure 1), 79 in the mainland Highlands (Region C: Figure 1), and 36 in the Southern Uplands (Region E: Figure 1). For the 36 birds tagged in the Southern Uplands, 27 were translocated as nestlings from Highland nests and subsequently released (hacked) as part of the SSGEP, and 9 were tagged as wild nestlings originating in the region.

November 2022 was the cut-off for the inclusion of data, and 66 tags were still transmitting data at the cut-off date, but only 42 were still in their dispersal phase; all movements were censored by territory settlement [5]. Tracks from the tag records were created by joining sequential locations and filtering out track fragments that did cross open water. Rarely, there would be a large time gap in the records, and sequential records could be separated by many hours; if the interval was more than three hours, that portion of track was removed. GPS/GSM tags can produce records at a rate of one per minute [62,63]. Despite this intensity of data supply and other tags' data without such frequent records, some tracks over stretches of sea were composed of multiple tracks, so they were combined into a single track to avoid creating many shorter tracks for one sea crossing. Tracks crossing any stretch of sea were clipped at the coast, and their lengths and day number recorded. The day number was the day in the year: for example, 1 February is day 32.

3. Results

The movements of satellite-tagged birds during natal (juvenile) dispersal within Scotland and northern England are shown in Figure 3. Superficially, but confirming the predictive capacity of the GET model [3], there was broad agreement between the records of dispersing birds (Figure 3) and the GET model's preferred habitats (Figure 2, see also Appendix A in [29]).

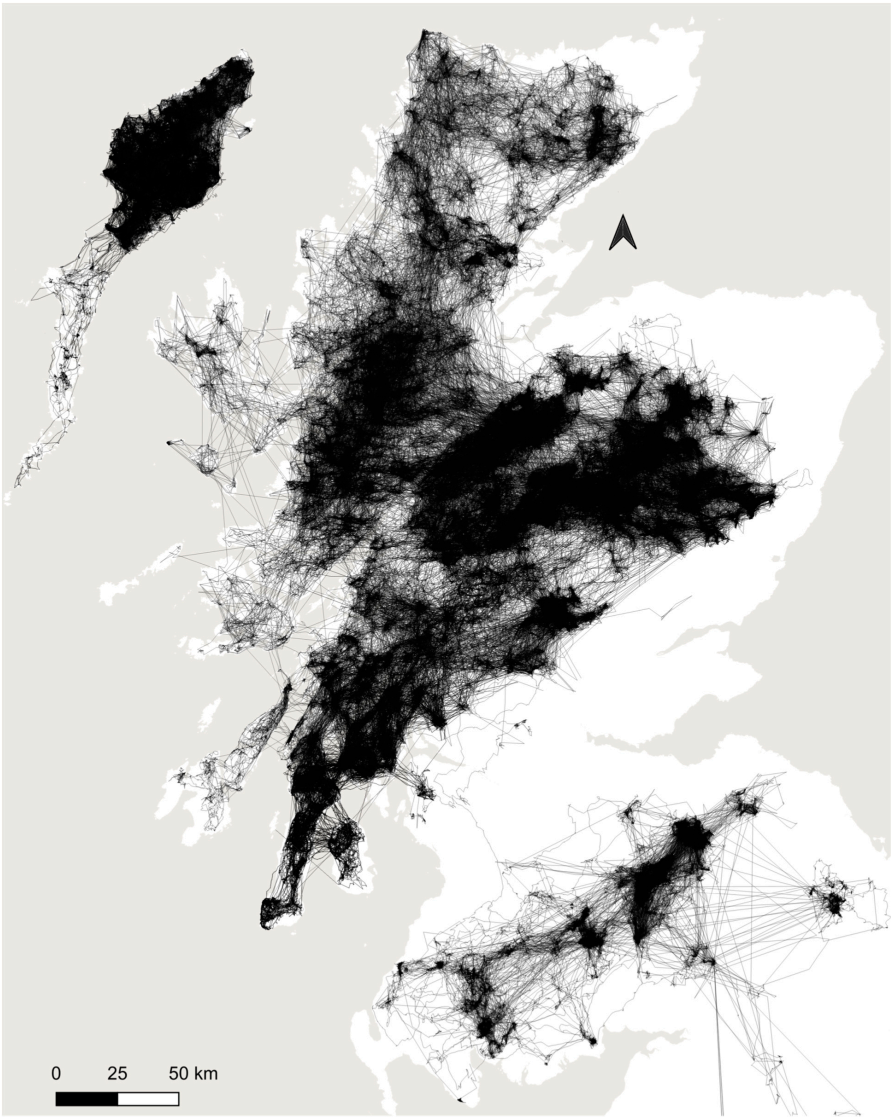

Figure 3. Golden eagle flight lines during natal dispersal from satellite telemetry records across Scotland and northern England. Contains Ordnance Survey data © Crown copyright and database right 2020.

3.1. Hypothesis 1, a Terrestrial Barrier

The GET model predictions of the suitability of the terrestrial habitat (Figure 2) confirmed the expected influence of two geological boundary faults (the Highland Boundary Fault and the Southern Uplands Fault), creating largely unsuitable Lowlands (Midland Valley) (Figure 1). There are some small patches of potential suitable habitat between the two Faults (Figure 2), which were visited occasionally by tagged birds from the Highlands (Figure 3). Nevertheless, there were no movements of birds tagged as nestlings in the Highlands across the Highland Boundary Fault and the Lowlands into the Southern Uplands (Figure 3). The individual tracks showed that birds typically approached the Highland Boundary Fault and then either flew along it or turned back quickly, hence the sharp influence of this fault, influencing GET habitat preference and the corresponding eagle movements (Figures 2 and 3).

There was one movement of a wild fledged bird (tag 583) from the Southern Uplands to the Highlands (Figure 3) out of the 36 birds fledged or hacked there. This eagle originated, as a 2015 nestling, in the southwestern Southern Uplands and moved north, into the Highlands, on 7 March 2016, in a long flight via an isolated patch of upland habitat within the Lowlands. Unfortunately, it was probably illegally killed in the eastern Highlands in mid-May 2016, 230 km north of its natal site [30].

Incidentally but similarly on the unsuitability of lowland habitats, there were also reductions of flight records (Figure 3) in the northeastern parts of the Highlands region (Figure 1), where upland vegetation and predicted GET habitat suitability peter out (Figure 2), giving way to flat lowland habitats often dominated by farmland [57]. Because the change from the northeastern Highlands to the northeastern lowlands is more gradual, there is a less obvious boundary for the flight lines.

3.2. Hypothesis 2, Limits to Crossing Seawater

National data and seasonality: The track lengths (i.e., the extent of seawater crossed) showed that, from a sample of 23,143 flights, less than one in one thousand flights over the sea exceeded 16.2 km (Figure 4). For context, there is at least 22 km of sea across the Solway Firth from good GET habitats between southwest Scotland and northwest England (Figures 1 and 2), at least 24 km across the Minch between the nearest Inner Hebridean island (Skye) and the Outer Hebrides (Figures 1 and 2), and 22 km from the most southwestern Highlands (Mull of Kintyre) to Northern Ireland. Seasonal changes in sea crossings showed a primary peak around March, with a secondary lower peak in autumn (Figure 5).

Isolation of the Outer Hebrides: No satellite-tracked birds tagged as nestlings moved between the Outer Hebrides and the Inner Hebrides or mainland Highlands (Figure 1), in either direction. Three tagged birds from the Outer Hebrides made several possible but apparently aborted attempts to fly towards the mainland Highlands (Figure 6). These were identified as flights that turned towards the Highlands and flew out to sea but then sharply returned (Appendix A).

Movements from the main Outer Hebridean islands in the north (Lewis and Harris) to southern islands of the archipelago were surprisingly rare, even when all the tagged birds originated on Lewis (north of Harris). There were only 12 crossings across the Sound of Harris (at maximum c. 13 km, ignoring islands within the Sound) to southern islands, made by four tagged birds (of 33) with all returning north (Figure 6, Appendix A).

Connectivity between the Inner Hebrides and the Highlands: There were many movements involving 24 tagged birds across the sea to and from the Highlands' mainland and the Inner Hebrides and across the numerous sea lochs (Figure 7). These records showed that: (a) movements across sea lochs in the Outer Hebrides (Figure 6) frequently occurred elsewhere; (b) there were many movements across the sea within the Inner Hebridean islands and with the mainland (Highlands region: Figure 1); (c) hence, there was no evidence for any disconnection between the Inner Hebrides and Highlands regions.

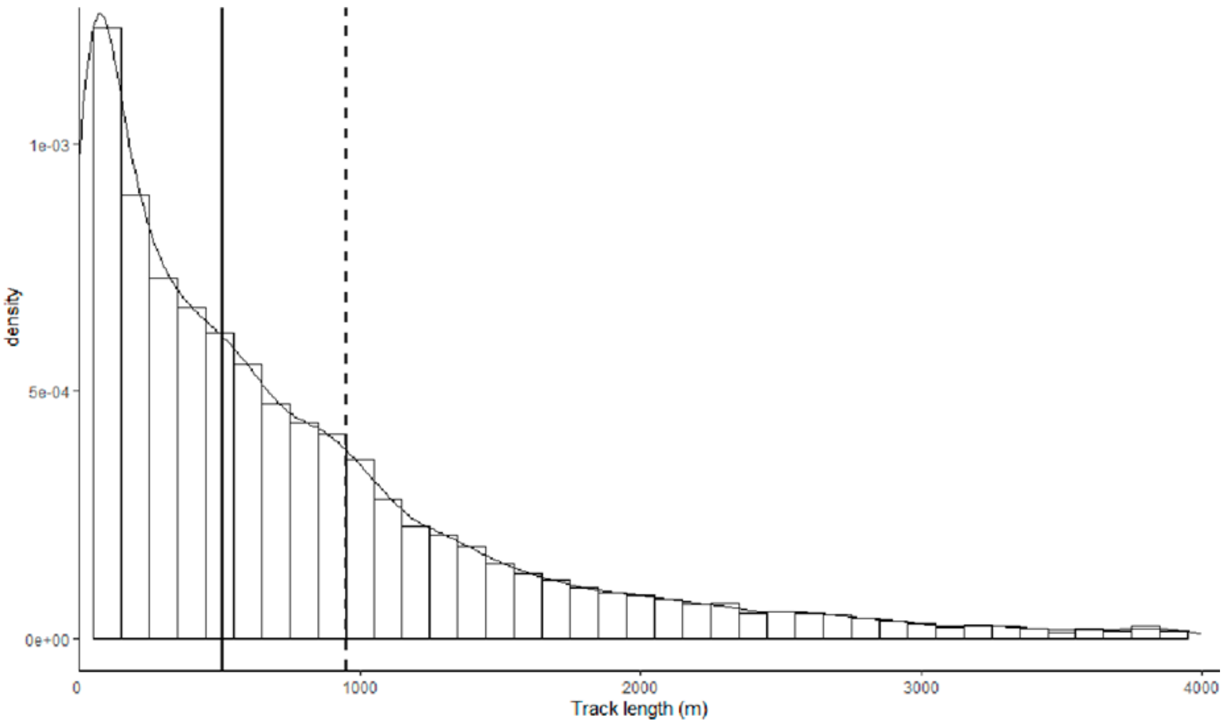

Figure 4. Histogram showing track lengths for sea crossings against their density. Count = 23,143; mean = 950.1 m (dashed vertical line); median = 509 m (solid vertical line); 5% quantile = 19 m; 95% quantile = 3361 m; 99% quantile = 7336 m; 99.5% quantile = 9175 m; and 99.9% quantile = 16,220 m.

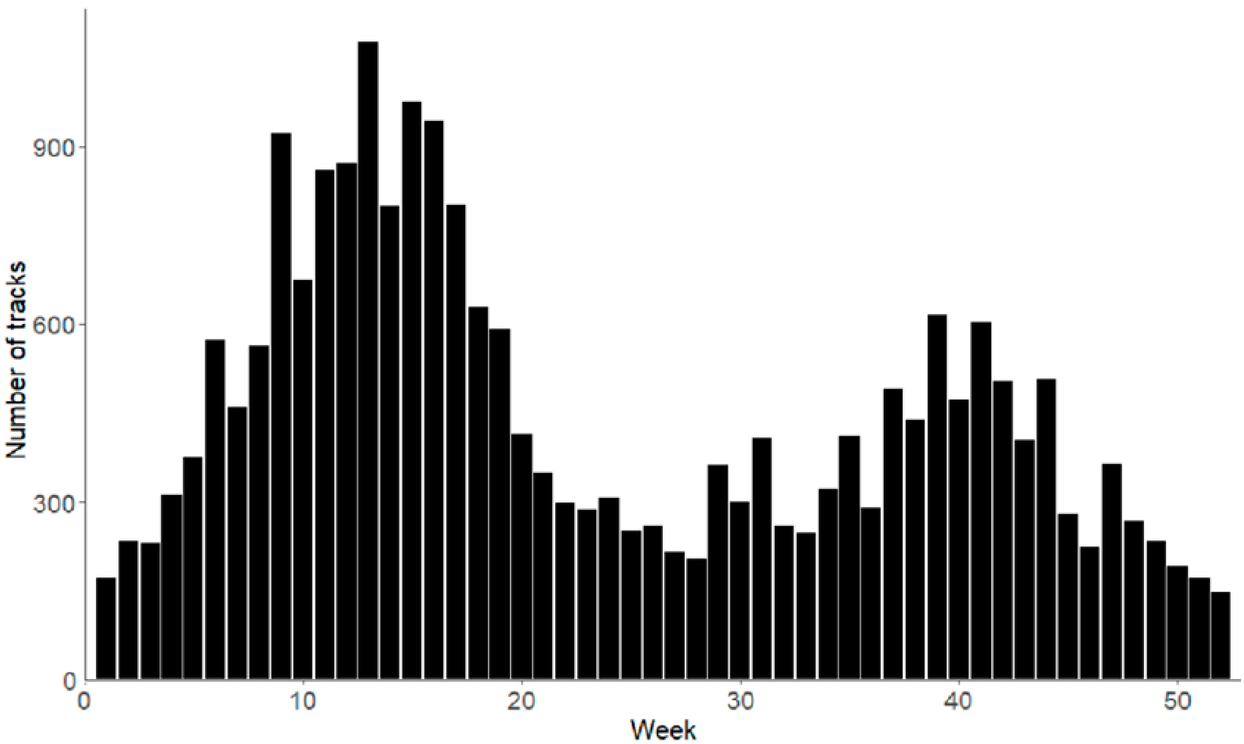

Figure 5. Histogram showing the seasonal distribution of the number of sea crossings (tracks). Week 1 = first week of January.

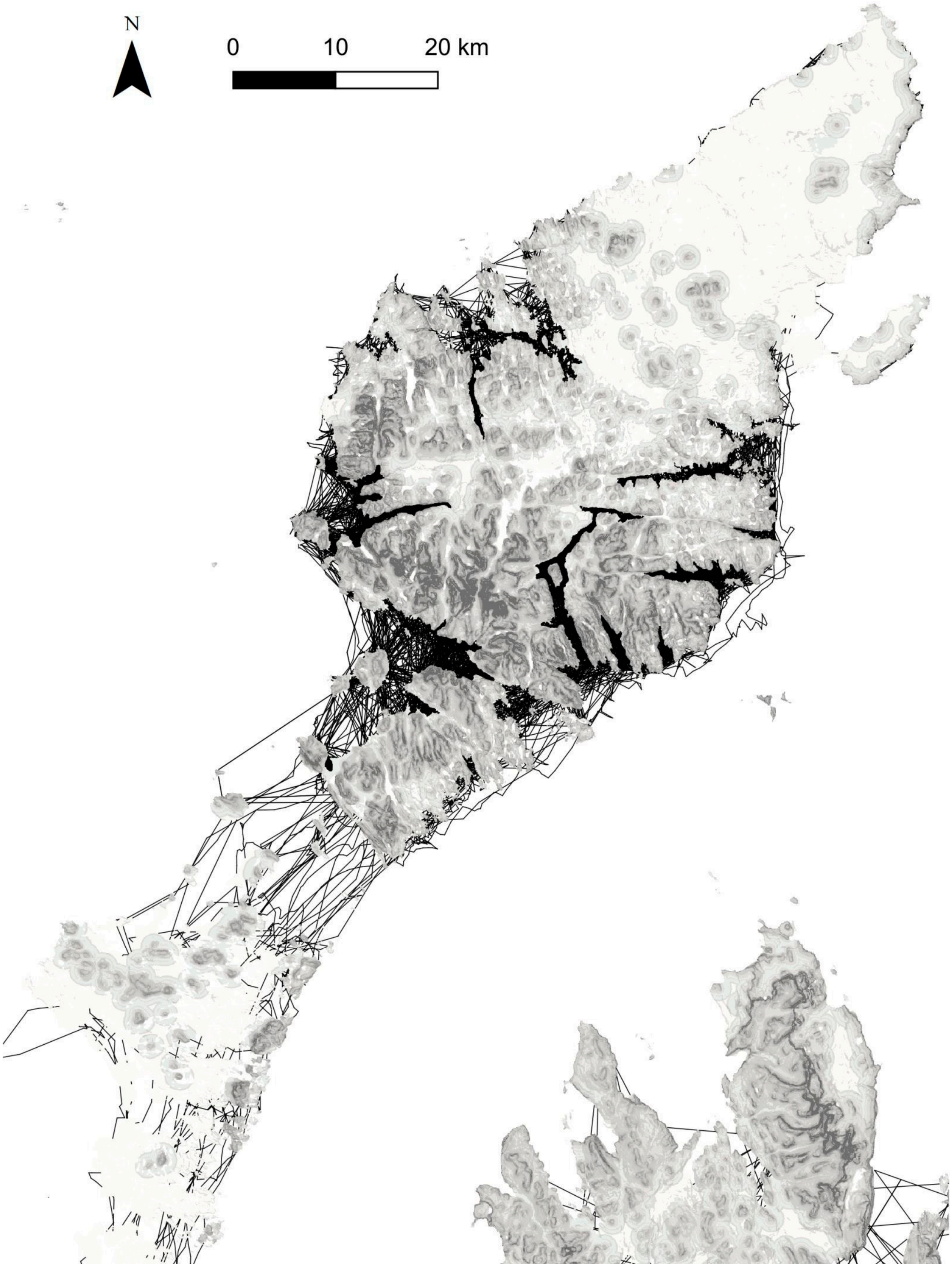

Figure 6. Movements of satellite-tagged birds across the open sea and sea lochs in the northern Outer Hebrides. The terrestrial backdrop shows the GET model's predictions, with darker grey being higher GET scores, predicting a higher preference. The largest terrestrial expanse shows the northern islands of Lewis and Harris (connected terrestrially, with Harris to the south). The sea channel in the south shows the Sound of Harris, dividing Harris from more southerly islands, with North Uist being the largest southerly island, beyond smaller islands in the Sound of Harris. The land in the southeast shows the northern limits of the nearest Inner Hebridean island (Skye) (Figure 1). Figure 1 (Region A) shows the location of the Outer Hebrides. Contains Ordnance Survey data © Crown copyright and database right 2020.

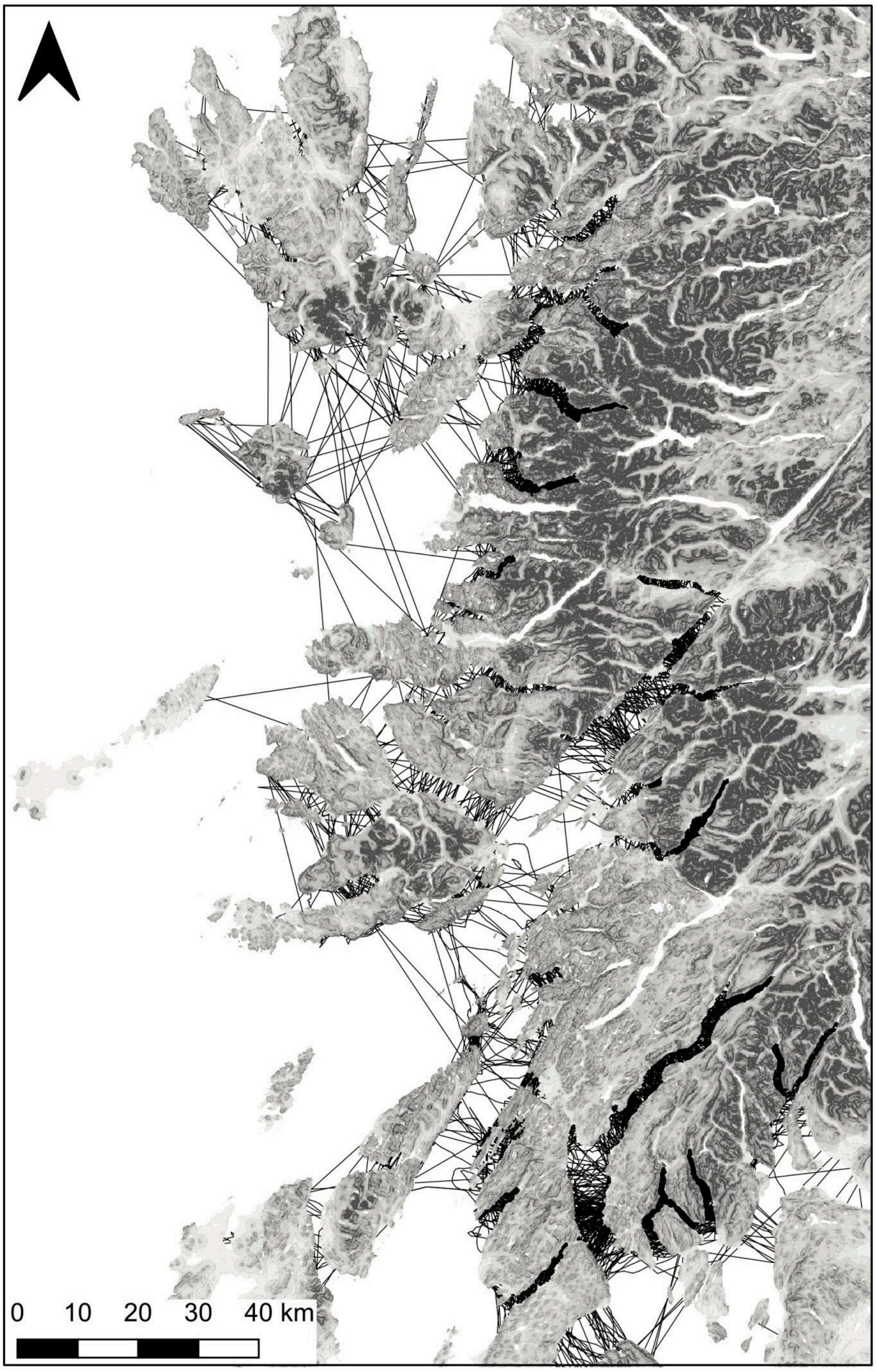

Figure 7. Movements of satellite-tagged birds across the open sea and sea lochs in the northern Inner Hebrides and the western Highland region (see also Figure 1). The terrestrial backdrop shows the GET model's predictions, with darker grey showing higher GET scores, predicting a higher preference. Contains Ordnance Survey data © Crown copyright and database right 2020.

Sea crossings to the south of Scotland: Only four tagged birds crossed the 3.5 km of sea across the outer Clyde estuary from the intensively used southwestern Highlands to an upland outcrop within the Lowlands (the Renfrewshire Heights), and all of them returned to the Highlands after varying durations of stay there (the longest was 38 d) (Figure 8). The apparent reluctance of golden eagles to cross the Clyde estuary to the Renfrewshire Heights was not mirrored for other sea lochs of a similar extent in the area (Figure 8). There were many examples of sea crossings at least as wide as the Clyde estuary in the southwestern Highlands. There were some movements of birds using the largest of the Clyde Islands (Arran) as a stop-over (Figure 8), but these few birds returned to the Highlands. It is approximately 5 km across the Clyde estuary from the Kintyre peninsula to the Isle of Arran. Tag 925 made the crossing 54 times before eventually settling in a range on the Kintyre peninsula. Four other birds made the crossing from Kintyre to Arran, but they made only two or three return crossings. None of the birds making the crossing from the Kintyre peninsula to Arran continued across the wider part of the Clyde estuary to the Renfrewshire Heights. Arran currently has six pairs of golden eagles, but no offspring from these ranges have been fitted with a tracking device, so we do not know if birds fledged on Arran make the crossing to the Renfrewshire Heights.

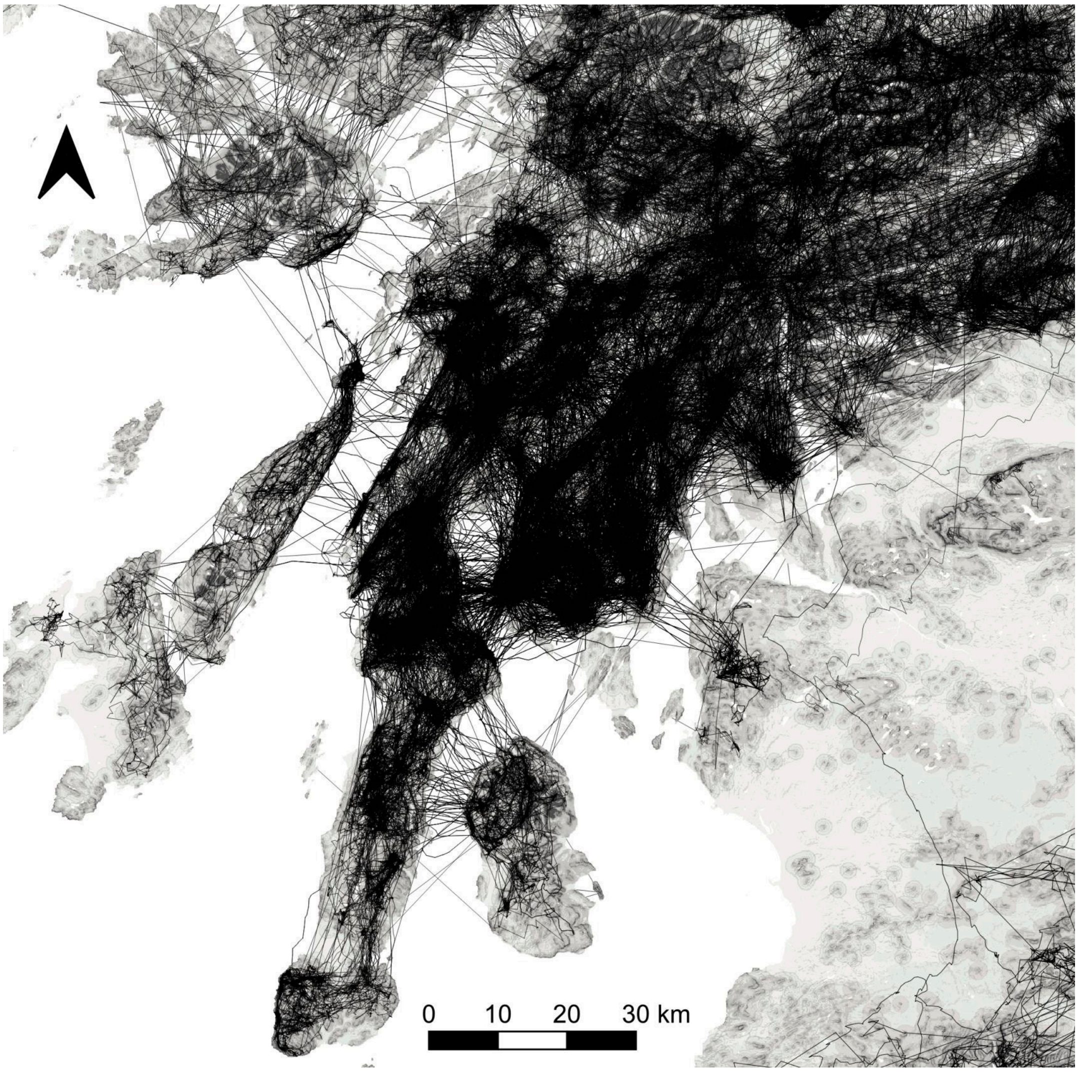

Figure 8. Movements of satellite-tagged birds in the southern Inner Hebrides, southwestern Highlands, the Clyde Islands, the Lowlands, and (extreme southeastern corner of the graphic) the Southern Uplands (Figure 1). The terrestrial shaded backdrop shows the GET model's predictions, with darker grey showing higher GET scores, predicting a higher preference. The peninsula with an outcrop of upland habitat (and higher GET scores) in the Lowlands, jutting into the extended Clyde estuary (firth), is the Renfrewshire Heights. The largest of the Clyde Islands (Figure 1) is Arran, which currently supports six breeding pairs. The finger-like peninsula in the Highlands, to the west of Arran, is Kintyre. The single track between the Southern Uplands and the Renfrewshire Heights involved one tagged bird (tag 583), moving north from the Southern Uplands to the Highlands (Section 3.2). Contains Ordnance Survey data © Crown copyright and database right 2020.

Overall, no birds crossed the sea directly from the Highlands or used the Clyde Islands to move to the Southern Uplands (Figure 8).

3.3. Hypothesis 3, the Isolation of Southern Scotland

Movements from the Highlands: The records showed that no birds moved from the Highlands to the Southern Uplands across the largely unsuitable terrestrial habitats of the Lowlands (Figures 3 and 8). There were also no records of birds using the sea to cross from the Highlands or the Clyde Islands (Figure 1) to the Southern Uplands (Figure 8).

Movements between southern Scotland and northern England: There were no movements of tagged birds from the southwestern Southern Uplands to northwest England across the sea (the Solway Firth, 22 km between suitable GET habitats: Section 3.2). By contrast, terrestrially (Figure 1), there were several movements of five birds between the Southern Uplands and northern England (Figure 3). This included tracks to an area of predicted suitable habitat that crossed the political boundary between the two countries (Figure 1), with fewer birds going further south into other parts of northern England. All these birds returned to the Southern Uplands of Scotland. Two birds made what appeared to be a long (>80 km) joint flight to an area close to the site of the last breeding pair of golden eagles in the English Lake District. They stayed only one night, in early April 2022, and returned to southern Scotland the next day. Subsequently, one of these birds settled into a territorial range in the south of Scotland with a different individual.

4. Discussion

Considering our three hypotheses (Section 1), we confirmed hypothesis 1 that the Lowlands appeared to be a terrestrial barrier to movements from the more populated Highlands to the Southern Uplands, even if, occasionally, small areas of suitable habitat in the Lowlands were visited. The Highland Boundary Fault and the Southern Uplands Fault largely contributed to this region of unsuitable habitat. The Lowlands extend to around 75 km or more between the Highlands and the Southern Uplands.

On hypothesis 2, there was a limit to the extent of sea that golden eagles were prepared to cross. The maximum limit was apparently around 20 km, with less than one in a thousand tag tracks being greater than 16 km. While there were two examples of movements of birds, ringed as nestlings, just beyond a 20 km limit (Appendix A), there were no recorded flights of tagged birds between the Outer Hebrides and the mainland (Highlands) or the Inner Hebrides (the closest distance was 24 km). Based on the movements of satellite-tagged birds, following a genetic study [8], the Outer Hebridean golden eagles appear to be substantially isolated from their conspecifics in the rest of Scotland.

Golden eagles in the Outer Hebrides are apparently isolated by the expanse of sea, possibly exacerbated by westerly wind conditions off the Atlantic Ocean, which may help in restricting movements from the Inner Hebrides or the Highlands. A low genetic connectivity was suggested as being more likely through few movements from the Outer Hebrides to the Inner Hebrides and/or Highlands, rather than in the opposite direction ([8], see also Appendix A).

This isolation is probably not just a feature of the extent of sea to be crossed but also the golden eagle's biology. White-tailed eagles *Haliaeetus albicilla* can move freely between the Outer Hebrides and the Inner Hebrides and the Highlands ([25,64,65], Fielding et al., unpublished data), but this species is more associated with marine habitats than the golden eagle [65].

On the other hand, the recorded limit on golden eagles' willingness to cross the sea meant that the numerous sea lochs (fjords) in Scotland were not a barrier to golden eagle movements.

There were also many flights to and from the Inner Hebrides, the Highlands, and, to a lesser extent, the Clyde Islands, indicating a prospective connection between these regions, confirming previous genetic research [8].

A few eagles made the short sea crossing between the densely populated southwestern Highlands to the nearest outcrop of suitable habitat in the Lowlands (the Renfrewshire Heights), but they all returned to the Highlands, and none moved further into the Southern Uplands, the main breeding region in southern Scotland. This indicated a further separation of southern Scotland, in addition to the terrestrial barrier, from an absence of connection with the Highlands across the sea.

The seasonality of the sea crossings, peaking in spring, with a secondary peak in autumn, was like the seasonal distribution of young eagles ending natal dispersal through their first settlement in a territory [7]. This may not be a coincidence. It may further suggest that young eagles' movements associated with obtaining a territorial opportunity are more intensive during some times of the year and are relaxed during the summer, when the use of Temporary Settlement Areas (TSAs) away from territories is more common [66].

Our results supported hypothesis 3, on the isolation of the Southern Uplands of Scotland and northern England from the much larger numbers of birds in the Highlands [26]. This was because there were no records of satellite-tagged golden eagles during natal dispersal that moved from the Highlands to these more southerly regions, either across the largely unsuitable terrestrial divide of the Lowlands, or across the sea.

If there is a prospect for the re-colonisation of northern England from the south of Scotland (largely through the bolstering of numbers in southern Scotland from translocations under the SSGEP: Section 1), the telemetry records show that this is more likely to happen across the terrestrial divide between the two countries, to the northeast of England, rather than across the marine divide, to the northwest of England.

It is important to emphasise that our records were from the natal (juvenile) dispersal phase of transience and so refer to Juvenile Dispersal Distance (JDD). The JDD is typically much greater than Natal Dispersal Distance (NDD) (e.g., [25,65]). The NDD is the movement (linear distance) between the fledging (natal) location and the first reproductive or potential reproductive location e.g., the first settled occupied territory [67,68]. In many raptors, especially in genera with larger species such as *Aquila* and *Haliaeetus*, most movements affecting gene flow, demography, and population/sub-population limits are most influentially due to the NDD rather than breeding dispersal (movement between successive breeding locations) [6,23,69,70].

In a sample of thirty-nine birds, the median estimates of the NDD of golden eagles in Scotland were 30 km for males and 59 km for females or 38 km averaged across the sexes, with a significant difference between the sexes. The maximum estimates were 82 km for males and 87 km for females [6]. The records of the JDD were typically much higher [30].

Hence, the JDD and especially the NDD [4] probably also operate in conjunction with physical barriers to restrict population or sub-population expansion. The JDD affects how much of Scotland and beyond is explored by dispersing young eagles. If the JDD is small, this must reduce the rate and potential for range expansion. However, even if the JDD is extensive, geographical range expansion will be slowed if the NDD is smaller. For example, observing some dispersing birds from southern Scotland venturing south into northern England does not necessarily mean that they may settle there to breed (leading to sub-population expansion), particularly if the NDD is less than the distance between the two areas.

Another biological feature, social attraction [71], may also play a role in restricting the connectivity between different regions. Social attraction suggests that the abundance of breeding conspecifics acts as an attractive component of habitat selection for young birds and so may influence decisions on territory settlement, even in species such as the Spanish imperial eagle *Aquila adalberti* [71], which, like the golden eagle, is not regarded as a "social" species in its breeding distribution.

For example, this may partly explain why releases of white-tailed eagles into eastern Scotland did not result in the establishment of a substantial east coast sub-population. Many released white-tailed eagles explored the west of Scotland, where there was an established population through earlier releases, and remained there to settle and breed [72].

In the present study, any influence of social attraction is most likely to apply to the empirical reluctance of wild-bred golden eagles from the highly populated Highlands to settle, or even explore, the poorly populated Southern Uplands.

In conclusion, following our overarching objective (Section 1), the Scottish population appears to be composed of three relatively isolated sub-populations. The largest is in the Inner Hebrides and in the mainland (Highlands) north of the Highland Boundary Fault; the second is the large Outer Hebridean sub-population; and the third, and much smaller and more vulnerable, is the southern Scotland sub-population.

We also found that the basis for the SSGEP was justified, in its active translocation of Highlands birds to the Southern Uplands, to reinforce and expand the territories there, rather than relying on natural expansion [54]. The telemetry data show that any natural expansion from the abundant Highland resource is unlikely. The southern Scotland sub-population appears to be isolated by a combination of geography and biology. Birds have to travel considerable distances over unsuitable habitat and at distances that probably exceed the typical NDD. The social attractiveness of the more abundant Highland sub-population may also discourage wild-bred Highland birds from moving to southern Scotland. By contrast, currently, the translocation of northern nestlings, hacked into the Southern Uplands under the SSGEP, is proving successful, with several new territories established since the project's inception in 2019 (C. Barlow, pers. obs.; Fielding et al., unpublished data, [7]). None of the 27 birds hacked into the Southern Uplands have crossed the Lowlands (Midland Valley).

Of wider application, we found that there were obvious geographical deterrents to dispersing golden eagles moving across unsuitable habitat boundaries when there is an expanse of poor golden eagle habitat. We estimated the extent of such geographical barriers to movement during natal dispersal. In a likely combination with features of the species' biology and history, this has apparently created three sub-populations in a relatively small country, geographically, albeit with considerable internal geographical variation. Our study examined a Scottish population that is resident, but it may encourage similar research elsewhere using the tool of satellite telemetry.

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Data Availability Statement: Due to the continued illegal persecution of golden eagles in some parts of Scotland [30] and the sensitivity of the ongoing reinforcement of the vulnerable southern Scotland sub-population through the SSGEP, our data are not being made public. However, they may be requested upon consultation directly with, and at the discretion of, the corresponding author.

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Appendix A

Details of apparently aborted attempts by three birds tagged on the Outer Hebrides to cross to the Highlands mainland or the Inner Hebrides

Tag 1071 made a nine-minute flight on 4 March 2022 at 12:40, flying 3 km east towards the mainland before turning back. Nine minutes later, at 13:03, she again turned to the east but this time only getting 1 km from the coast. On 24 September 2022, at 11:57, she made another abortive presumed flight towards the mainland. This time she turned back once she was 1 km from the coast. Also on 4 March 2022, at 12:20, 1072 (female) made a 14 min flight 2.6 km towards the mainland. Tag 1072 is unusual in being the only tagged eagle to make a flight out from the west coast into the Atlantic Ocean. On 15 October 2020, at 12:01, she flew 2.5 km out to sea before returning to the island. Tag 1153 made a fourteen-minute flight 2.6 km out towards the mainland at 12:03 on 5 March 2022, followed by an eight-minute flight, starting at 12:24, heading out 1.5 km from the coast. Later the same day, at 14:47, he undertook a six-minute flight 1.2 km east. On 14 April 2022, he made a six-minute flight, to the same location as the 12:03 flight on 5 March 2022, which took him 1.2 km out to sea, before returning.

Thirty-three birds were tagged on the Outer Hebrides in Lewis, and these few apparent attempts at sea crossings were consequently unusual.

Movements within the Outer Hebrides: few tagged birds went south from the northern islands of Lewis and Harris

Of the 33 tagged eagles tagged on the northern island of Lewis, only 4 moved across the Sound of Harris channel separating the islands of Lewis and Harris from the more southerly islands of the archipelago—including (north-to-south) North Uist, South Uist, Benbecula, Barra, and Mingulay (Figure A1). All four returned to Harris and Lewis. Only tag 1071, a female, crossed the 13 km channel between Harris and North Uist without stopping off at one of the five main islands in the channel between them. Tag 1071 was also the only bird to cross the Sound of Barra and flying towards the southerly limit of the Outer Hebrides, Mingulay, before returning to Harris.

An apparent reluctance to cross from Harris was not because the southerly islands lacked a suitable habitat. The southerly chain of islands has approximately 26 occupied golden eagle ranges, most on the Uists, with one on Mingulay. Lewis and Harris currently support around 69 occupied ranges ([26], R. Reid, pers. obs.). The density of breeding golden eagles is slightly higher on the Uists than on Lewis and Harris, and productivity is also slightly higher on the Uists. There are few areas of upland habitat outside the core territories on the Uists compared to Lewis, where there are large areas of upland foraging habitat at the edge of territories in the north (Lewis Peatlands) where breeding densities are lower. Most of the new territories and re-occupations of vacant territories in the last twenty years have occurred on Lewis and Harris, not on the Uists, so the recent opportunities for settling into new territories have mostly been north of the Uists, especially on Lewis (R. Reid, pers. obs.). This may contribute to why there may be a greater tendency for golden eagles to disperse more from the Uists to Lewis than in the other direction (also see below).

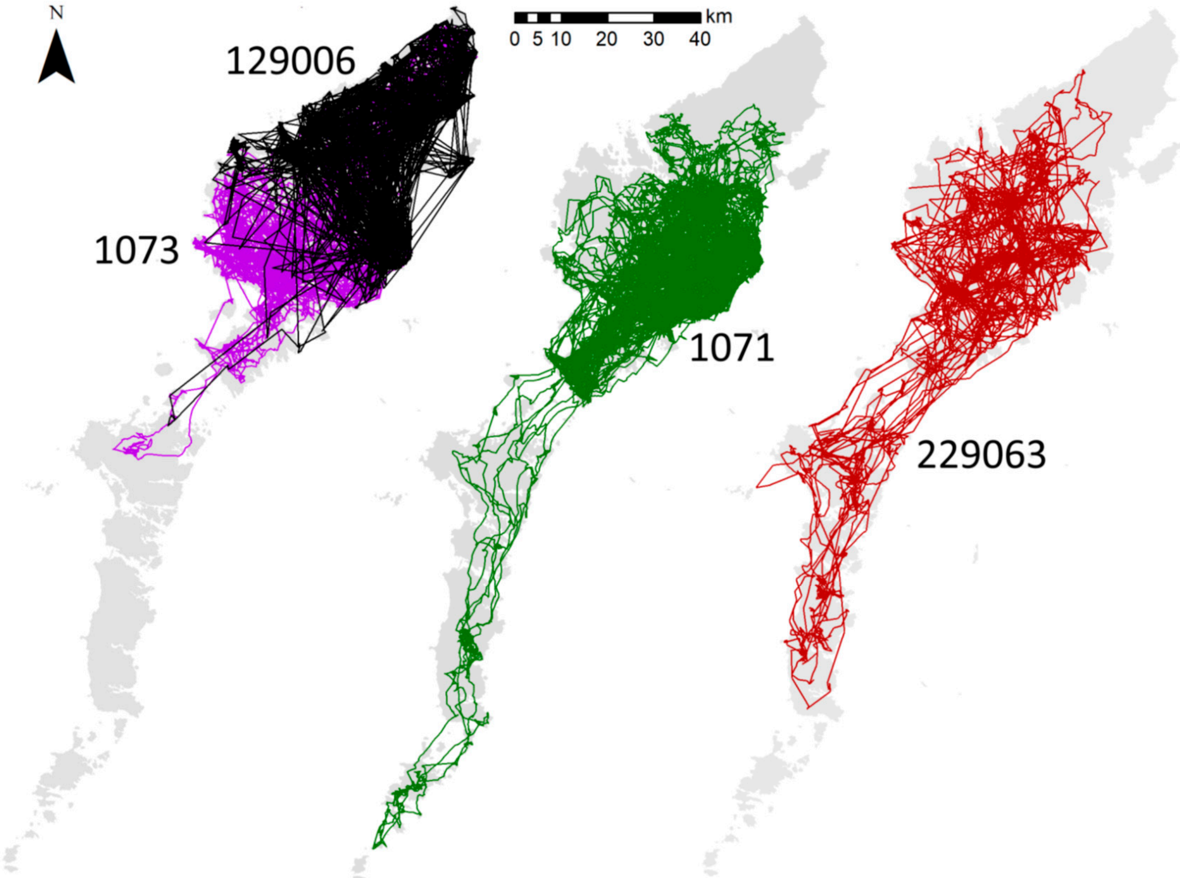

Figure A1. Tracks of four tagged birds in the Outer Hebrides between the northern islands of Lewis (where all the birds had been tagged) and Harris (more southerly) to and from the southern islands of the archipelago. Contains Ordnance Survey data © Crown copyright and database right 2020.

Additional information from ringing in the Outer Hebrides

Over a twenty-one-year period, 2003–2023, there have been 109 golden eagle nestlings ringed on the Uists and 78 ringed on Lewis and Harris. Of the ten territory holders of known origin on Lewis, seven are from Lewis or Harris natal sites and three are from natal sites in the Uists. From nestlings ringed during this period on Lewis or Harris, there has been only one recovery in the Uists (R. Reid, pers. obs.).

A nestling ringed in the Uists in 2006 was recovered dead on the mainland (Highlands) in 2015, as an adult, and was likely breeding there. This is the only example we know of a bird crossing from the Outer Hebrides to the Highlands and probably settling to breed there. A nestling ringed in Lewis in June 2015 was found dead on a beach in March 2018 at Ardmore Point, the closest point of northwestern Skye (Inner Hebrides) to the Outer Hebrides (Figure 6). This sub-adult bird may have died during an attempt to cross the Minch and was washed up on Skye.

Patagial wing-tag record of nestling translocated to Ireland later moving back to Scotland

Separate to sea crossings involving the Outer Hebrides, we are also aware that a nestling that had been translocated from Scotland to Donegal in northwest Ireland, as part of the Irish reintroduction project [27], was identified subsequently by its patagial wing-tag moving back to Scotland. This involved a sighting on Rathlin Island, off the Northern Irish coast, before being seen later on the Isle of Mull in the Inner Hebrides (L. O'Toole, pers. comm.). This record strongly indicates that the bird had crossed the 22 km of sea between Northern Ireland and the southwestern Highlands (Section 3.2).

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