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Between a rock and a large place: the importance of multi-scale geomorphological features to seabird nest site selection

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The importance of habitats to animal, and, in particular, bird conservation, has long been recognized (Martin et al. 2007, Yorio 2009, Oppel 2018). From the study of habitat has emerged the importance of geodiversity (Hjort et al. 2015, Hunter 2017, Malcolm and Hunter 2017, Gray 2021). The relationship between geodiversity and biodiversity is a fundamental, yet often-overlooked aspect of ecology; for example, we recently demonstrated that several seabird species show preferences for particular small natural features of potential nest sites (Eveillard-Buchoux et al. 2019 and Fig. 1). These intriguing results led directly to the next question: Do larger-scale geomorphological features also contribute to nest site selection?

Proximity to food resources is obviously a major determinant of nest site selection at large geographic scales (e.g., Nelson 2002, Barrett and Lorentsen 2006). Assuming that potential sites for nest selection are adequately close to food resources, and that summer thermal conditions are not limiting, e.g., in southern North Atlantic populations (Stokes and Boersma 1998, Kulaszewicz and Jakubas 2018), the most important criterion for successful seabird nesting is protection from predation (Bried and Jouventin 2002, Brooke 2018). Such protection is afforded at the largest spatial scale by isolation in the form of distance from large land masses, which can contain more predators than small islands (Bried and Jouventin 2002). At an intermediate spatial scale, the slope of the nesting facies (e.g., cliff face) can also variably isolate the nest from predation, depending on slope steepness. Finally, at the smallest spatial scale, that of the nest itself, isolation from predation may be more or less strengthened by the degree of enclosure, such as in a burrow or beneath a rock overhang (Eveillard-Buchoux et al. 2019). We therefore defined three components of isolation, at increasing spatial scales: nest, slope, and land mass (Fig. 2). We then characterized 20,580 nest sites at 17 nesting locations for eight seabird species (see Fig. 3 for details of bird and colony numbers) in Brittany, France, according to three isolation-related, increasing-scale geomorphological features: degree of enclosure (open or closed), elevation of facies (high > 40 m, moderate 20–40 m, low < 20 m) and type of slope (flat ≤ 30°, intermediate, and vertical ≥ 70°, as measured by clinometry and laser telemetry), and type of land mass (small island [<1 km²], medium islands [>1 km²], continental outcroppings). Land mass size was chosen as the most relevant large-scale spatial isolation variable because small islands were not colonized by humans, whereas larger ones were, independent of the distance from the mainland. All of the islands were members of continental archipelagos (0.7–18 km from mainland). These three geomorphological feature scales are depicted in Fig. 2.

Our results (Fig. 3) showed a surprisingly clear pattern for all eight seabird species, when interpreted from the standpoint of spatial modes of protection from predation. The three smallest and likely most vulnerable species (Jones et al. [2008] and size refuge theory; see Day and Abrams [2002] and Harper and Peck [2009] for reviews and references), Shearwater, Storm Petrel, and Puffin, preferred enclosed nests on small islands, at all slope classes. Small islands are likely to contain fewer species and smaller populations of terrestrial predators such as rats, cats, foxes, weasels, minks, etc. compared to larger land masses. This relationship is borne out in the predator-presence–island-size data: six of the 17 sites (all large land masses) contained land-based predators (cats, weasels, rats); seven sites (all small islands) contained no terrestrial predators; the remaining four could not be characterized with certainty. All of the sites were subject to aerial predation by gulls and crows. The "small land mass" reduction in predator pressure can be expected to be more pronounced with decreasing island size and increasing island distances from the mainland. A

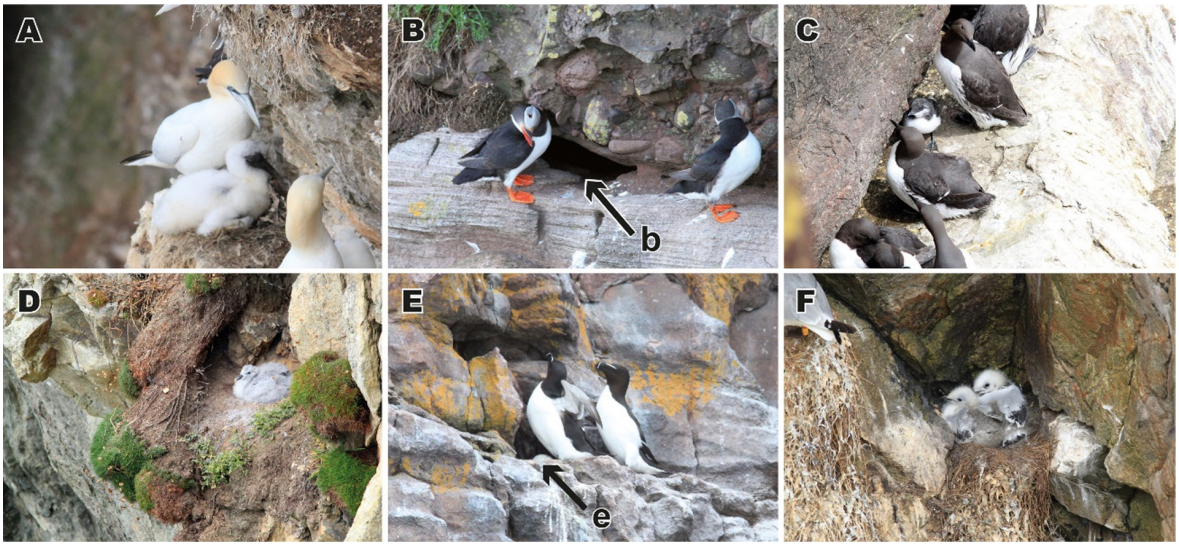

FIG. 1. Nest types of the seabird species studied: (A) Gannet, (B) Puffin (b, burrow entrance), (C) Guillemot, (D) Fulmar, (E) Razorbill (e, egg), and (F) Kittiwake.

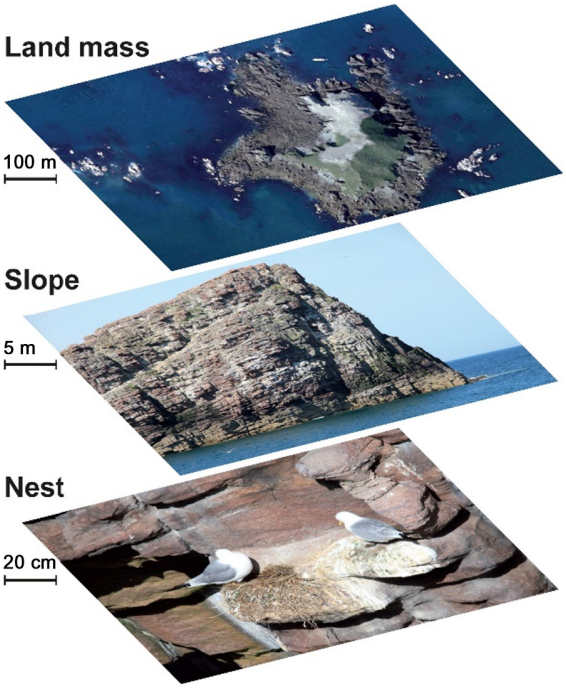

FIG. 2. Increasing scales of geomorphological features involved in seabird nest site choice.

preference for small islands is thus a first-level spatial defence against predation. Preference for enclosed nest sites is a second level of spatial defence, reducing the probability of success for many land predators and seabird predators (e.g., Gulls [*Larus fuscus*, *Larus marinus*, *Larus argentatus*] and Corvids [*Corvus corone, Corvus corax*]). Shearwater, Storm Petrel, and Puffin use natural terrain micro-features (rock formations, abandoned rabbit burrows) or even create their own enclosed nest sites in the absence of such features (e.g., Puffin burrows).

Kittiwakes are not among the largest seabird species, so they are also vulnerable to land predators. However, their clear preference for vertical cliff faces greatly reduces the threat from these predators and also serves to reduce predation intensity of some seabird predators such as gulls. In contrast, the equally vulnerable Guillemot and Razorbill achieve the same result using either of two alternative strategies: enclosed nests on small islands in the absence of vertical cliffs, or open nests on vertical cliff faces for all land mass types.

The largest, least predator-vulnerable species, Gannets and Fulmars, showed the least specialization in nest site choice. Gannets have predominantly open nests regardless of land mass or slope type; Fulmars are the most complete generalists, exploiting all nest site, slope, and land mass types. Taken together, these results show a direct relation between intrinsic seabird vulnerability to predation and geomorphological selectivity of nest site.

Closer inspection of Fig. 3 reveals a more subtle, yet nonetheless important type of relationship. In addition to their 'stand-alone' effects, site characteristics at the three spatial scales can be either *compensatory* or *complementary*, depending on the nesting species. For example, a steep slope compensates for the reduced isolation of open nests (e.g., 100% of the continental Kittiwake, Razorbill, Guillemot, and Fulmar nests were on high vertical slopes), whereas a closed nest compensates for the absence of a steep slope (e.g., Puffins and Razorbills nesting on open island terrain). On the other hand, a

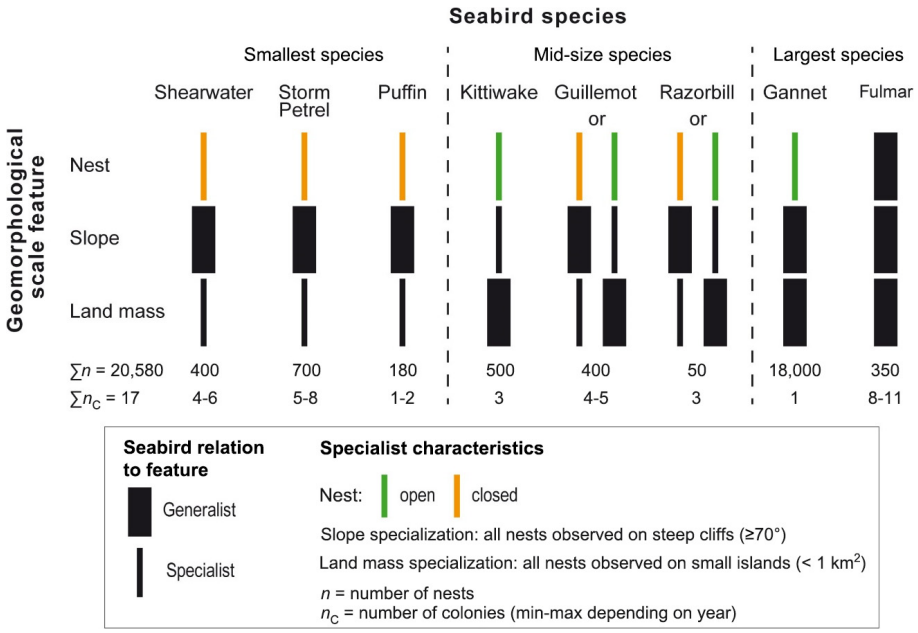

FIG. 3. Summary of nest-site geomorphological features at three spatial scales, for each seabird species studied. Puffin, Shearwater, and Storm Petrel are nest-level and land-mass-level specialists, preferring enclosed nest sites on small islands; they are slope generalists; the preceding features providing sufficient isolation from predators. Kittiwake are steep slope specialists, this feature providing sufficient predator isolation to allow them to use open nest sites on island or continental cliffs. Guillemot and Razorbill use one of two isolation options: open nests on steep cliffs (island or mainland), and enclosed nests on open terrain (small islands only). The largest of the species studied, Gannets and Fulmars, are the least vulnerable to predation and also show the least requirement for isolation, using open nests on all slope and land mass types.

steep slope may complement a high elevation, and a high elevation or steep cliff may complement the "distance from mainland" (island) effect.

Seabirds play important roles as environmental sentinels, in the linking of terrestrial and marine ecosystems, in conservation awareness, and ecotourism (Burger and Gochfeld 2004, Parsons et al. 2008, Mallory et al. 2010, Beninger et al. 2011, Paleczny et al. 2015). Surprisingly, there is a dearth of rigorous, species-specific studies on the non-food related spatial determinants of nest site choice in seabirds (see Eveillard-Buchoux et al. 2019). Our results demonstrate that the contribution of landscape features on seabird nesting site choice, and therefore seabird reproduction, is based on a combination of specific geomorphological features at several spatial scales.

Landscape features are obviously not the only criteria that influence nest site selection. The presence and density of conspecifics, food resource availability, and anthropic pressure are also likely determinants. Future studies should examine each possible criterion and evaluate its contribution to nest site selection. The seabird species studied in the present work represent a particular set of ecological circumstances: they are at or near their southern nesting limit in the temperate summer North Atlantic, and therefore thermal stress (i.e., shelter from cold winds, rain, hail, etc.) is not a major factor in nest site choice. Similarly, all of the studied sites were legally protected from direct anthropic disturbance, and this factor could be important in less-protected jurisdictions. Indirect anthropic disturbance (fishing impact, maritime navigation) could be another important determinant of nest site selection at large geographic spatial scales. These may be key factors in nest choice in other areas of the North Atlantic, and we look forward to additional work in this direction, with a view to the elaboration of a more complete, species-by-species paradigm of nest choice, with the aid of predictive tools such as Random Forest Models (e.g., Fox et al. 2017).

The present study demonstrates that geodiversity is an important factor in the distribution of seabird nesting locations. Since nesting is the foundation of seabird reproduction, any effort to mitigate the worldwide decline in seabird numbers (Paleczny et al. 2015) should include geodiversity considerations. These early results indicate that a promising new field of research awaits exploration, at the intersection of geomorphology and seabird ecology. Although seabird ecologists intuitively understand the importance of geographical features to nest site selection, this work is the first attempt to systematically characterize these features, and establish their relative importance to different seabird species. We look forward to investigations of other geographic areas and species, and to work on the interaction of these

purely physical site characteristics with the biotic environmental variables.

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All data used for this manuscript have been archived in Zenodo at https://doi.org/10.5281/zenodo.5163957.