

BIOLOGY OF THE CHARADRIIFORMES

The Beringian Connection: Speciation IN THE Herring Gull Assemblage OF NORTH AMERICA

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Gulls, especially the large white-headed gulls (“LWHGs”, i.e., Herring Gull and the like), have a kind of bad reputation among most birders. Adults of most LWHG taxa display a mean facial expression, and their scavenging behavior (with a certain taste for innocent little ducklings) does not contribute positively to their popularity. In addition, they are considered impossible to identify, especially in the many immature plumages. Nevertheless, there are a few hardcore bird-identification aficionados who will even admit in public that gulls are definitely among their favorites.

Even on the most boring winter day, studying a small group of gulls is always rewarding. Plumage variation among LWHGs is bewilderingly complex, but the more you look the more you see and understand. Consider for instance the recently published *Gulls of Europe, Asia, and North America* (Olsen and Larsson 2004). At first glance, the uninitiated will find this book incomprehensible, but after the initial shock, they will appreciate it for being a bountiful source of new information. For the serious gull specialist, however, this book is a collection of plates, pictures, and text, all to be verified against one’s own knowledge. Nothing more and nothing less, and outdated before it was printed.

Why is gull identification so complex? First of all, most LWHG taxa do not reach adulthood until three to five years of age. In the meantime, they will have displayed ten or more different plumages (see Olsen and Larsson 2004). Second, we now assume that many of the LWHG taxa are evolutionarily very young and still evolving as we speak. Third, most of the LWHGs are highly adaptive and very good flyers, and population ranges and sizes have most likely never been stable.

Since the early 1990s a number of articles have been published about the taxonomic affinities of LWHG taxa on the basis of genetic information (Snell 1991, Wink et al. 1994, Bell 1996, Panov and Monzиков 1999, Chen et al. 2001, de Knijff et al. 2001, Liebers et al. 2001, Crochet et al. 2002, Liebers and Helbig 2002, Crochet et al. 2003). Recently, Yésou (2002) discussed the relevance of these studies in his excellent detailed taxonomic revision of predominantly the



This article examines the evolutionary relationships among the widespread, aggressive, and adaptable Herring Gull and its congeners in the “large white-headed gull” complex. Recent molecular studies—summarized in this article—demonstrate surprising and sometimes counterintuitive relationships within the Herring Gull complex.

American Herring Gull. *Appledore Island, Maine; May 2004.* © Garth McElroy.

Eurasian members of this assemblage. Unfortunately, none of these articles contained sufficient genetic data to disentangle recent migration processes from more-ancient evolutionary processes. In addition, they all included only a limited number of taxa or only a few individuals per taxon. At that time, Yésou could not have known that we were almost finished with a study aimed at sorting out the complexity of the Herring Gull assemblage, using a detailed DNA-based population approach including nearly all of the relevant taxa from Eurasia and Northern America (Liebers et al. 2004). Here we would like to expand Yésou’s review, concentrating on the North American species. This article is not an overview of the identification of these LWHG taxa. Instead, it is an examination of the his-



American Herring Gull. *Wells, Maine; February 2003.* © Garth McElroy.

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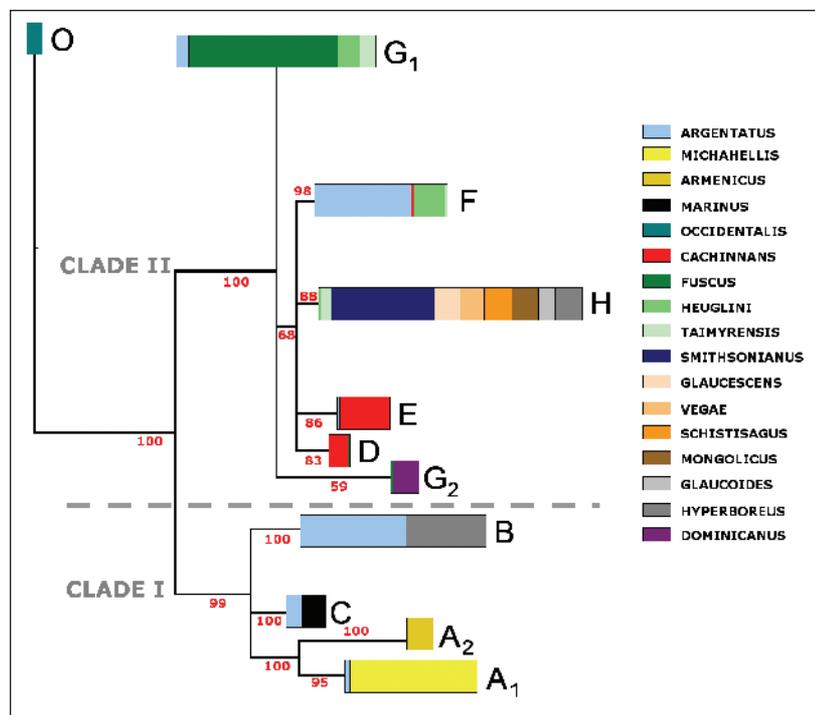


Fig. 1. This simplified phylogenetic tree is based on mtDNA sequences. Bars representing groups of closely related sequences are labeled A–H. Western Gull (O) was designated as the outgroup. Numbers along each branch are Bayesian posterior probabilities (expressed as percentages). In plain English, they can be considered to be measures of statistical support. Within each bar, sub-bars are used to indicate different sampling locations of the gulls, their sizes being proportional to the frequency in the entire sample. Colors represent different large white-headed gull taxa as indicated in the legend and correspond with the geographical distributions as shown in Fig. 3. © Peter de Knijff.

torical and biological processes that may have given rise to the diversity of LWHGs in North America.

THE GLOBAL PICTURE

Based on earlier gull DNA studies by Wink et al. (1994) and Crochet et al. (2002), we anticipated little mitochondrial DNA (mtDNA) differentiation among most gull taxa. Therefore, we decided to analyze a larger-than-usual mtDNA fragment from as many individuals per sampling location as possible. DNA from 410 individuals sampled at 53 locations was sequenced for two different mitochondrial regions: (1) the rather slow-changing cytochrome B (cytB) gene of 1,143 nucleotides; and (2) the very fast-evolving (so-called “hypervariable”) Region I, which is 430 nucleotides long. Using a combination of population genetic, phylogenetic, and phylogeographic statistical analyses we were able to (1) build a phylogenetic tree (Fig. 1) connecting all 160 different sequences, and (2) reconstruct the most likely model of differentiation and colonization (Fig. 2) explaining the present distribution (Fig. 3) of nearly all LWHG taxa (for full details, see Liebers et al. 2004). On the basis of the genetic differences within the cytB gene only, we could also put some provisional dates on some of the most important events in

LWHG evolution, summarized below.

Due to a single population-fragmentation event, at least 300,000 years before present, an ancestral population was split into two populations, one of which drifted toward the North Atlantic and contained the ancestor of all sequences contained in Groups A–C (Fig. 1). These four closely related groups of sequences are also referred to as Clade I (Groups A–C; Fig. 1) sequences. The other population probably remained in the Aralo-Caspian Area and contained the ancestor of all Clade II (Groups D–H; Fig. 1) sequences. By means of a range expansion, starting 190,000 years ago, the North Atlantic population expanded southward to establish an isolated Macaronesian (i.e., the Canary Islands and Madeira) refugium in which we find the founder of all Group A sequences.

Another range expansion, starting 164,000 years ago, resulted in a central Siberian population containing the original founder of Groups F, G, and H from the Aralo-Caspian population. About 122,000 years ago, the North Atlantic population started to expand farther northeast, by means of a series of multiple range expansions. A first expansion resulted in a northern European Herring Gull (*argentatus*) population containing Group B and C sequences. A second expansion led to the first Eurasian *hyperboreus* (Glaucous Gull), also with Group B sequences. At about the same time, a single long-distance colonization event resulted in the settlement of gulls with Group A sequences in Anatolia (*armenicus*; Armenian Gull) from the Macaronesian refugium (*atlantis*; Atlantic Yellow-legged Gull).

Due to three independent range expansions, birds from the central Siberian population expanded in different directions. The first, starting 100,000 years ago, resulted in a second, more-southerly *argentatus* population containing Group F sequences. The second expansion from the central Siberian population, starting about 65,000 years ago, gave rise to an eastern Siberian population with Group H sequences, which eventually expanded farther east into North America, and south along the northeastern Asian Pacific coast. The third expansion, commencing about 47,000 years ago, gave rise to the northern European *fuscus* (Lesser Black-backed Gull) population with Group G1 sequences, which subsequently expanded into the breeding range of *argentatus*.

At later times, most likely starting just before the last glacial maximum, about 25,000 years ago, the much younger Group H, carrying taxa such as *smithsonianus* (American

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mtDNA to the next generation) are infertile, which is in line with Haldane's Rule (1922), which predicts that first-generation hybrids carrying identical sex chromosomes (males, in birds) are fertile, whereas the heterogametic sex (females, in birds) are infertile or display reduced fertility. This pattern could explain why we do not see sharing of mtDNA lineages, whereas Bell (1996, 1997) clearly demonstrated extensive sharing of autosomal gene products (protein variants which are coded for by nuclear DNA).

- The fact that we do not see sharing of mtDNA types between Western and Glaucous-winged, in contrast to Bell's observation of extensive sharing of protein variants between these two taxa, could be due to the fact that we screened only 10 individuals each of Western and Glaucous-winged. This possibility can easily be tested by analyzing more birds, especially from the hybrid zone.

Either way, it is clear that this hybrid zone is remarkable among the LWHG taxa. It demonstrates that two gull taxa, which are phenotypically distinct and do not share a recent common ancestry, can nonetheless hybridize extensively and apparently have been doing so for a long time.

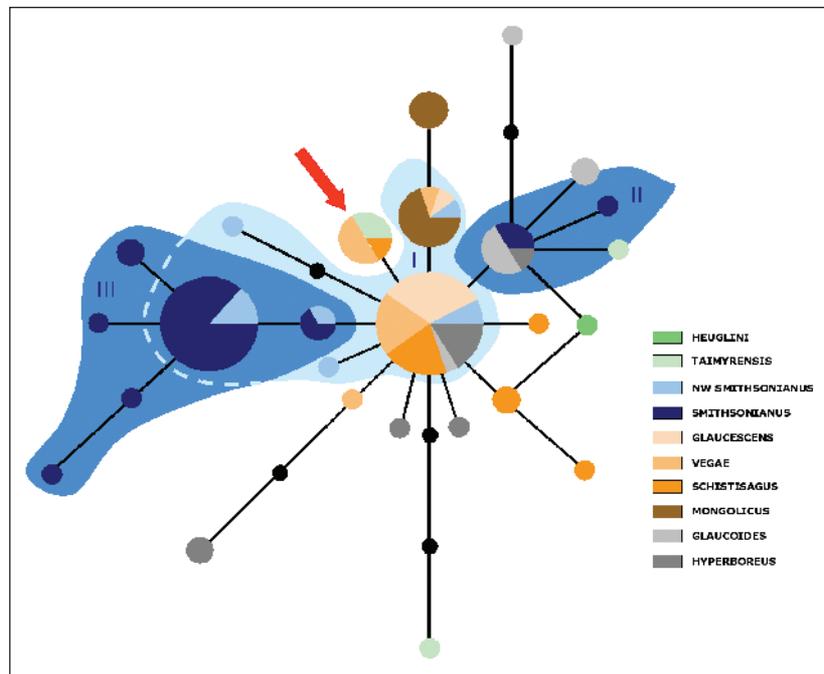


Fig. 4. This detailed network depicts all different Group H sequences in the Beringian group. The most ancestral sequence (i.e., the one closest to all other sequences according to the complete phylogenetic tree; see Fig. 1) is indicated with a red arrow. Each multicolored circle represents a single specific mtDNA sequence type, its size being proportional to the frequency of that sequence type in the entire sample. Small black dots represent inferred single-mutation steps (sequence types not found). Colors represent different "large white-headed gull" taxa as indicated in the legend and correspond with the geographical distributions as shown in Fig. 3 and the bars in Fig. 1, with one exception: Pale blue, used here to indicate sequences obtained from American Herring Gull individuals sampled in Alaska and the North West Territories, is used to indicate European Herring Gull in Figs. 1 & 3. The three different areas indicated as I–III represent three different groups of sequences observed among American Herring Gull. © Peter de Knijff.

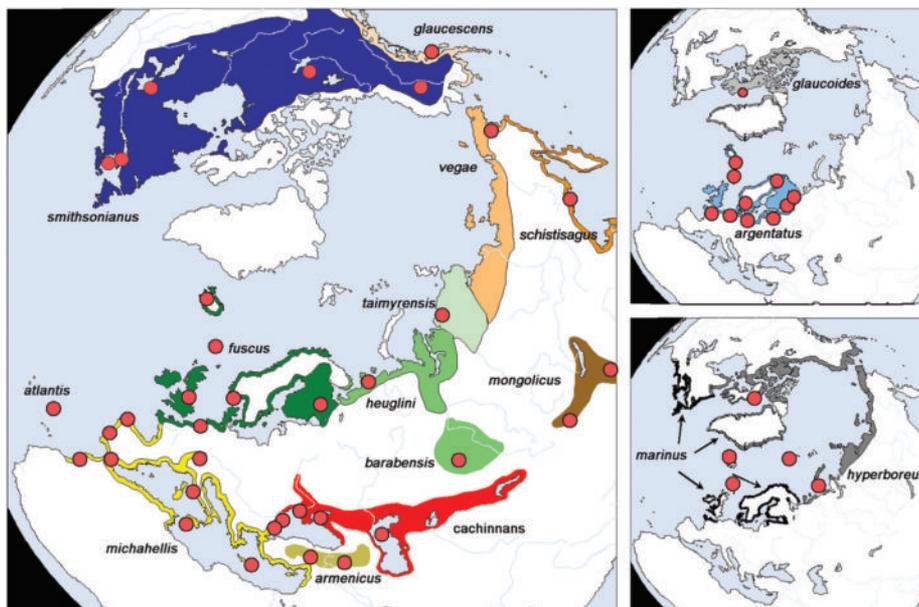


Fig. 3. The approximate current breeding ranges and sampling locations (red circles) of the large white-headed gull taxa that we investigated are shown here. For clarity, extensive overlapping ranges are shown on separate maps. Ranges of Western Gull and Kelp Gull are not shown. See Fig. 1 for a key to the colors. Adapted from Liebers *et al.* 2004.

Yellow-footed Gull

We were unable to obtain samples from Yellow-footed Gull. However, based on the results of Crochet *et al.* (2002), it is likely that Western and Yellow-footed are closely related taxa. More DNA results are needed to provide a detailed picture of the genetic affinities between the two taxa. It has been suggested by Pierotti and Annett (1995) that Yellow-footed and Western Gulls are closely related to Kelp Gull. Our results clearly show otherwise. Kelp Gull shares common ancestry with western Palearctic Lesser Black-backed Gulls (*fuscus* group) and/or Tundra Gull (*heuglini*). In any case, it is not closely related to Western and Yellow-footed, if our mtDNA results are a reliable indicator.



Western Gull. Los Angeles County, California; March 1998. © Brian E. Small.

The Iceland–Kumlien’s–Thayer’s Gull Complex

The taxonomic affinities among the various populations of these high-Arctic breeders remain very puzzling. Apart from the discussion about the scientific credibility of studies of whether Kumlien’s Gull (*Larus glaucoides kumlieni*) is a valid taxon (Snell 1989), there is almost no reliable genetic data for this complex. It seems logical to conclude that Thayer’s, Iceland, and Kumlien’s are very closely related, with Kumlien’s assuming an intermediate position with respect to distribution and phenotype (discussed in detail by Weir et al. 2000, Howell and Elliott 2001, Howell and Mactavish 2003). We have analyzed only a small number of Kumlien’s from Home Bay, Baffin Island ($n=7$), and Crochet et al. (2002) present data from a single individual each of Iceland, Kumlien’s, and Thayer’s. As is clearly shown in Fig. 4, we find no differentiation between Kumlien’s and the other Beringian taxa, corroborating the sparse results of Crochet et al. (2002). Obviously, many more individuals from different locations should



Thayer’s Gull. Churchill, Manitoba; May 1991. © Peter de Knijff.

be analyzed. The suggestion by Snell (2002) to isolate DNA from skins sampled at breeding colonies is a good one, at least for obtaining mtDNA sequence information. We are less optimistic that this approach would allow sequencing of nuclear DNA, and we hope that a young and ambitious scientist will pick up this Arctic challenge and collect new samples. To this end, we hereby offer our laboratory facilities once the samples have been obtained.

Glaucous Gull

It has always been assumed that the various subspecies of the Glaucous Gull form a continuous circumpolar metapopulation. However, our DNA results show a different picture, which we cannot explain satisfactorily at the present time. All Eurasian Glaucous Gulls have Group B mtDNA sequences that are similar to or shared with nominate Her-



Yellow-footed Gull. Salton Sea, California; May 1992. © Brian E. Small.

ring Gulls (Fig. 1). However, the Baffin Island Glaucous Gulls show only Group H sequences. A number of equally likely scenarios, all assuming introgression at one stage of colonization, could explain this surprising disparity (see Liebers et al. 2004). Considering the minor phenotypic differentiation among Glaucous Gull populations, we find it unlikely that this genetic divide truly reflects the evolutionary history of the taxon. Again, more sampling, especially from west-Arctic and central-Arctic North American breeding colonies, coupled with screening of nuclear DNA fragments, should reveal the true history of the taxon.

Herring Gull

In Europe, the American (*smithsonianus*) Herring Gull had long been seen as the mother of all European (*argentatus*, *argenteus*) Herring Gulls. However, recent research shows

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Glaucous Gull. *St. Johns, Newfoundland & Labrador; January 1993.* © Peter de Knijff.

that there is little doubt that *smithsonianus* is genetically distinct from *argentatus* and *argenteus* (Crochet et al. 2002, Liebers et al. 2004). The latter two taxa carry mtDNA sequences predominantly from Groups B, C, and F (Fig. 1), whereas all *smithsonianus* display Group H sequences. Within Group H, most *smithsonianus* (>90%) have sequences not shared with the other Beringian taxa (Group III sequences; Fig. 4). It is obvious that we can recognize three genetically different *smithsonianus* sub-groups:

- The oldest sequences (the pale blue Group I sequences), which are shared with other Beringian taxa. These sequences are found only among individuals collected in Alaska and the North West Territories.
- Group II sequences found among birds from Ontario. These sequences are shared with Glaucous and Kumlien's from Baffin Island.
- Group III sequences found at all colonies. This group of related sequences bears the sign of what is called a star-like phylogeny: From a single very frequent sequence, many other sequences emerge with single-mutation differences. Such a pattern is a clear sign of a young and rapidly expanding population.

This pattern of sequence heterogeneity among *smithsonianus* strongly suggests that the westernmost *smithsonianus* colonies have, on average, a different mtDNA sequence type compared to other colonies. It was recently suggested (Jonsson and Mactavish 2001) that there are at least two phenotypically distinct *smithsonianus* populations present in North America. If this hypothesis is valid (it has also been suggested that this difference merely reflects differences between males and females wintering at different localities), it is difficult to

reconcile Jonsson and Mactavish's observations with our results because it is not known where exactly the two wintering populations (from Niagara Falls and Newfoundland) breed.

The small number of Group II sequences among Ontarian *smithsonianus* is more difficult to explain. They could be the result of recent introgression of arctic mtDNA sequences into *smithsonianus*, or they could simply be the leftover of an ancient relic population of *smithsonianus*. During the late Weichselian / late Wisconsin epoch (from 25,000 to 17,000 years ago), the southern half of North America was completely isolated from the Beringian area by a number of large ice sheets. It is not inconceivable that, since that time, a small and isolated *smithsonianus* was thriving in southern North America and that mtDNA sequences of those birds are still exclusively found in small numbers among the more-eastern populations. Recently, Chen et al. (2001) published a detailed summary of mtDNA sequence variation among 224 *smithsonianus* individuals sampled from the Great Lakes basin and from Prince Edward Island, areas from which most of our *smithsonianus* samples came. Although these sequences contained only 1,055 base pairs of the *cytB* gene and displayed less sequence variation, they yielded a few more *smithsonianus* sequence types, all falling into Group III. Thus, even with these additional samples, we could not refine our conclusions regarding the population structure of *smithsonianus*. Only extensive sampling and sequencing across the entire distribution of *smithsonianus* will reveal the true extent of its genetic differentiation.

California Gull

Although we were unable to obtain sequences from the California Gull, there is little doubt that this taxon is an integral part of the Beringian Group H. The short sequence



American Herring Gull. *Wells, Maine; February 2005.* © Garth McElroy.



California Gull. Ventura County, California; March 1999. © Brian E. Small.

published by Crochet et al. (2002) falls into the middle of this group. Obviously, sufficient samples of the two races of California Gull (*albertainensis* and nominate *californicus*) will have to be analyzed in detail before detailed conclusions concerning the true affinities between this taxon and the other Beringian taxa can be made.

Great Black-backed Gull

No one would have predicted that, at least in Europe, the Great Black-backed Gull mtDNA sequences would cluster together with nominate (*argentatus*) Herring Gull sequences in a distinct group (Group C) of mtDNA sequences, despite its uncontested distinct taxonomic position and marked phenotypic differentiation. Still, this result is what we and others (Crochet et al. 2002, 2003) have found. We were unable to sample Great Black-backed Gulls from North America. However, according to Crochet et al. (2002, 2003), their two Great Black-backed Gull sequences from North America do cluster with *smithsonianus*. And a single Great Black-backed Gull sequence published by Chen et al. (2001) of an individual sampled in Canada clusters, as all European Great Black-backed Gull sequences do, with nominate (*argentatus*) Herring. We assume that Great Black-backed Gull could be the founding father of all Clade I taxa and that the clustering of Great Black-backed Gull with some nominate (*argentatus*) Herring simply reflects the true shared evolutionary origin of these two taxa. The sharing of Group H sequence types between *smithsonianus* and Great Black-backed Gull individuals of North American origin could be due to secondary introgression of Group H sequences into expanding North American Great Black-backed Gulls. Since

the mtDNA sequences obtained by Crochet et al. (2003) are very short, they do not allow us to infer from which North American taxon the introgressed sequence could have come. Their conclusion that it derives from *smithsonianus* is unwarranted. Who could have guessed something as complex as this from a gull as distinct as *marinus*?

CONCLUSIONS

Without doubt, with the exception of Western and Yellow-footed Gulls, all large American gull taxa share a very recent common ancestry in eastern Siberia. Their close relatives are *vegae*, *schistisagus*, and *mongolicus*, with whom they form the Beringian Group H. When they entered North America, Western and Yellow-footed had already been there for at least a million years. But this has not prevented Western from hybridizing extensively with Glaucous-winged.

In numbers, geographic distribution, and genetic differentiation, *smithsonianus* is the most successful North American gull. It is quite distinct from other taxa and not closely related to Eurasian Herring Gulls. Full-species rank for *smithsonianus*, distinct from *argentatus* and *argentatus*, is clearly supported by our data and has also been suggested by Crochet et al. (2002). The arctic taxa remain very puzzling. A well-structured and systematic sampling from all Arctic-breeding taxa (including *smithsonianus*) is necessary in order to settle once and for all the puzzle of Thayer's vs. Iceland Gull. Why are Baffin Island Glaucous Gulls so different in their mtDNA from Eurasian Glaucous Gulls? We can only guess.

One thing is very clear. Despite all the current effort, a lot remains to be learned about the genetic affinities among all



Great Black-backed Gull. Appledore Island, Maine; 20 September 2004. © Garth McElroy.



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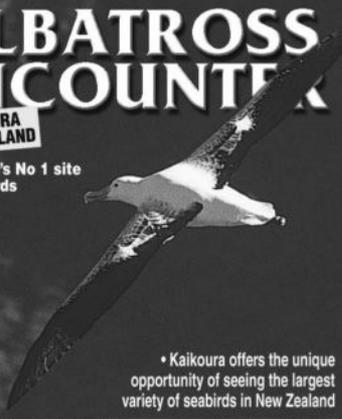
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large gulls. We sometimes have the feeling that we have raised more questions than we have been able to answer. On the one hand, this can be disappointing. On the other hand, it stimulates us to dig even deeper. Gulls are fun, not only on the beach, but also in the lab. Keep this in mind the next time, when on a very boring day, you decide to have a look at a small group of gulls.

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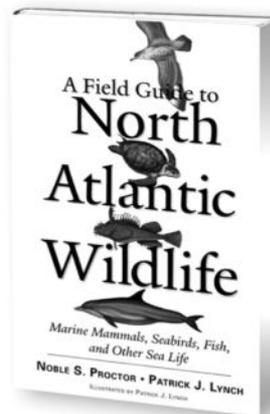
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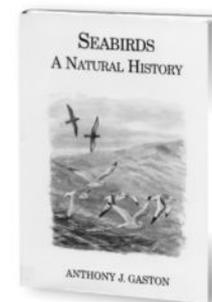


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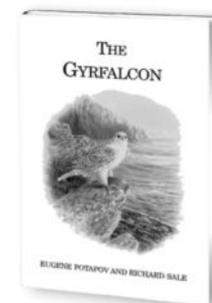


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