WHAT TO EAT WHEN FAR FROM HOME? A VAGRANT SEABIRD SELECTS NOVEL BUT ANALOGOUS PREY

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ABSTRACT

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Vagrancy in birds is an important mechanism contributing to range expansion and the establishment of new breeding populations. However, research on the ecology of vagrant individuals has been limited. From 2005 to 2021, a Red-billed Tropicbird *Phaethon aethereus*, far outside its usual range, was a summer resident at Seal Island, Maine, USA. In 2020 and 2021, we collected fecal samples from this individual and identified prey types consumed via DNA metabarcoding techniques, using 12S and 18S genes. We identified six fish species in the Red-billed Tropicbird fecal DNA samples, with Atlantic Saury *Scomberesox saurus* and Atlantic Mackerel *Scomber scombrus* contributing ~75% of DNA reads. To our knowledge, these two species have not previously been documented in the diet of Red-billed Tropicbirds, yet they were important in both years despite contrasting environmental conditions. Although it is quite possible that this vagrant individual had not encountered either saury or mackerel prior to its extralimital dispersal to the Gulf of Maine, these species share morphological and functional traits with known tropicbird prey elsewhere. Thus, despite occurring > 2,400 km from known breeding sites, this Red-billed Tropicbird was capable of selecting suitable prey in a variable environment.

Key words: dietary plasticity, DNA metabarcoding, Gulf of Maine, seabird diet, vagrancy

INTRODUCTION

Each summer from 2005 to 2021, a Red-billed Tropicbird *Phaethon aethereus* (hereafter RBTR) attended the seabird colony at Seal Island National Wildlife Refuge (43°53′24″N, 068°44′00″W) in Knox County, Maine, USA (Maine Bird Records Committee, 2021). Although RBTR are typically restricted to the tropical Atlantic, Indian, and eastern Pacific Oceans (Orta et al., 2020), this vagrant returned consistently to Seal Island despite its location more than 2,400 km from the species' nearest known breeding sites in the Caribbean (Lee & Walsh-McGehee, 2000). Although the Seal Island RBTR was never banded or marked, its consistent presence at the same island at highly predictable times of year—far beyond the species' typical range—suggests that a single individual was involved. The Seal Island RBTR consistently occupied a particular rock crevice, made highly vocal display flights, and, on multiple occasions, attempted to copulate with lobster trap floats (KCY & WLK, personal observations). These behaviors, paired with the reliable occurrence of the RBTR at Seal Island over 17 years, indicate that this record was not simply that of an accidental or storm-driven wanderer. Rather, the Seal Island RBTR appears to represent an (ultimately) unsuccessful attempt at range expansion of the species by a particularly widely dispersing individual.

Vagrancy as a mechanism of range expansion is not a new idea (Grinnell, 1922), and vagrant birds continue to be touted as "vanguards of range shifts" (Davis & Watson, 2018). While the distributions of all bird species have likely been influenced by vagrancy to some degree over time (Fjeldsa et al., 2020), the exceptional dispersal abilities of many seabirds make for numerous dramatic examples of range shifts within this group. Instances of seabird breeding range expansion across ocean basins are not rare and include, for example, the 20th-century colonization of the eastern North Pacific by Laysan Albatross *Phoebastria immutabilis* (Henry et al., 2021) and of the western North Atlantic by Manx Shearwaters *Puffinus puffinus* (Storey & Lien, 1985). Expanding populations are likely to produce more dispersing individuals; accordingly, vagrancy rates have been found to reflect population growth and/or the recent reproductive success of source populations (Veit, 2000; Zawadzki et al., 2019). For example, the recent expansion of Elegant Tern *Thalasseus elegans* breeding range to western Europe was preceded by a dramatic population increase of this species in North America (Veit et al., 2021).

Most vagrant individuals do not establish novel populations. The specific factors influencing the success of nascent populations remain poorly understood, but likely include the number of prospecting individuals, the distance from the source population, and the availability of suitable habitat and prey (Buxton et al., 2014; Lees & Gilroy, 2014; Oro et al., 2011). Following the first Gulf of Maine record of RBTR in 1986 (Maine Bird Records Committee, 2021), Veit (1988, 1989) suggested that RBTR were easily capable of traveling from the Caribbean to the Gulf of Maine and likely disperse beyond their known range far more frequently than they are observed and documented. However, he argued that the absence of breeding in the Gulf of Maine suggests that an unidentified factor has prevented their colonization of the region (Veit, 1988).

In response to recent and rapid environmental change, many taxa are expected to shift their geographic distributions, and the ability to do so may prove critical to species resilience (Barbet-Massin et al., 2012; Thomas, 2010). A better understanding of the factors that influence dispersal ability and range expansion is necessary to inform effective conservation measures; vagrant individuals could, thus, be viewed as valuable natural experiments that allow us to examine these potential limiting factors. Presented with a unique opportunity to determine the diet of a vagrant seabird, we noninvasively collected fecal samples from the Seal Island RBTR over two consecutive years for diet analysis using DNA metabarcoding. These results provide insight into the foraging flexibility of RBTR and provide an example of a vagrant individual adopting novel food resources.

METHODS

Field sampling occurred on Seal Island National Wildlife Refuge, 38 km off the coast of Rockland, Maine, USA (Fig. 1). Field work was conducted by researchers that reside seasonally on the island and all work was performed with the approval of the U.S. Fish and Wildlife Service and National Audubon Society Seabird Institute. Fecal samples were collected from fresh sheets of plastic wrap placed in the RBTR's regular roost site June–July 2020/21. The roost consisted of a crevice beneath a large, granite boulder, similar to many RBTR nest sites at Caribbean colonies (Boeken, 2016). The protected nature of the roost site, and the location of the site at least 600 m away from the main seabird colony (terns *Sterna* spp., Atlantic Puffins *Fratercula arctica*, Razorbills *Alca torda*, and Black Guillemots *Cepphus grylle*) allowed collection of samples free from any visually-identifiable contamination.

All fecal samples were collected with fresh, individually-wrapped wooden spatulas and were immediately placed into sterile collection vials containing 1 ml of DNA/RNA Shield (Zymo Research, Irvine, USA). DNA extraction, amplification, and sequencing methods were similar to those detailed in Fayet et al. (2021 and supplementary materials therein) and were led by

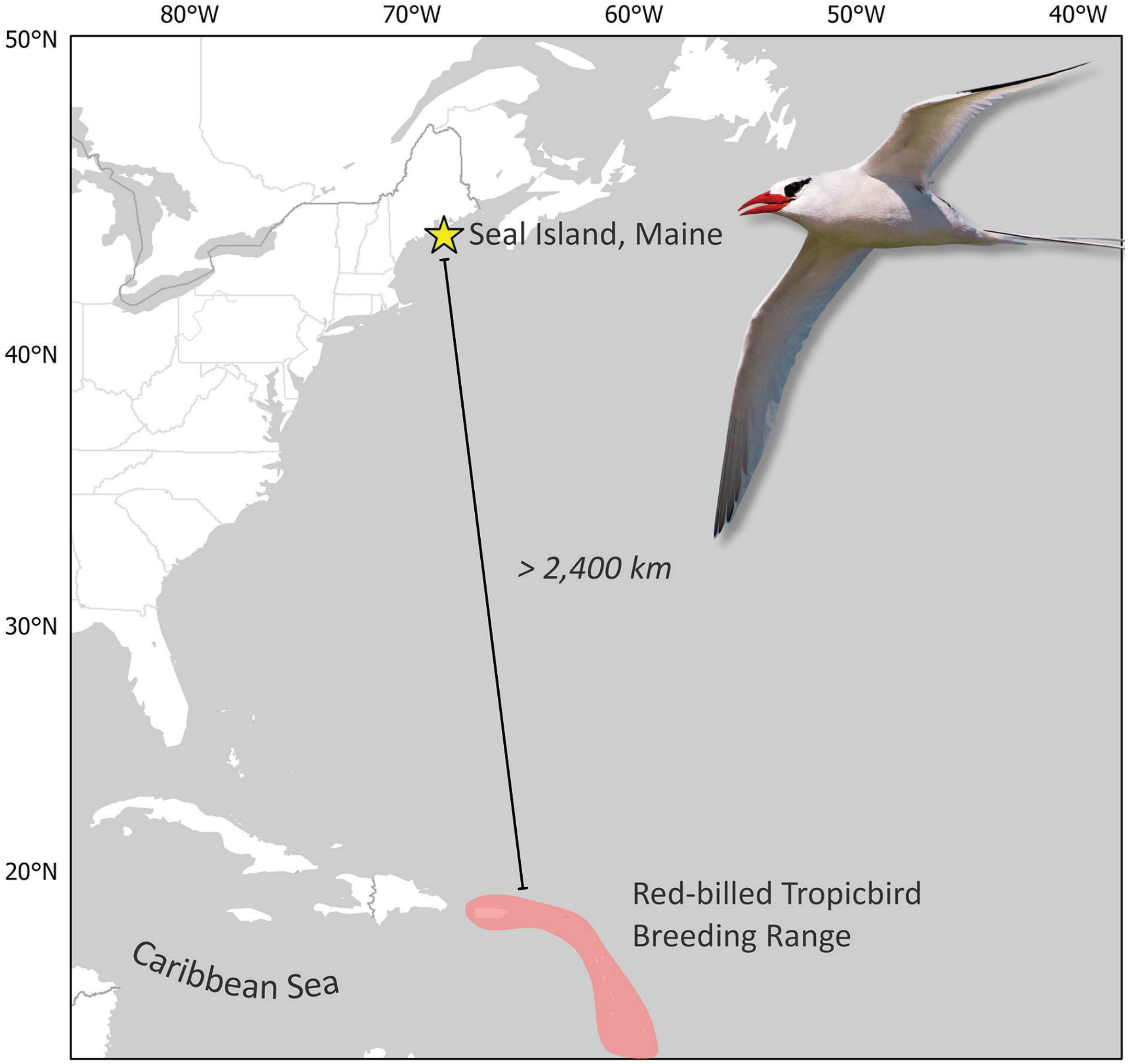

Fig. 1. Location of Seal Island, Maine, USA (star) compared to the nearest Red-billed Tropicbird *Phaethon aethereus* breeding sites in the Caribbean (pink). Inset image of the Seal Island Red-billed Tropicbird taken on 11 June 2015 by Keenan Yakola.

GVC. Fecal samples were homogenized, and DNA was extracted from samples using a Quick-DNA Fecal/Soil Microbe Miniprep Kit (Zymo Research, Irvine, USA). We attempted to characterize the RBTR diet using primers targeting two gene regions: (1) 18S to capture the occurrence of broad metazoan groups within the RBTR diet (McInnes et al., 2017); and (2) 12S to obtain higher taxonomic resolution of fish prey (Miya et al., 2015). For both primer sets, DNA sequences were amplified using 4.6 µl of template DNA and two-step PCR. We monitored for potential contamination by testing field-, extraction-, and PCR-blanks. Fecal DNA samples and blanks were sent to the University of New Hampshire for sequencing on an Illumina HiSeq 2500 (Illumina Inc., San Diego, USA).

Following sequencing, demultiplexed reads were imported into Qiime2 (Bolyen et al., 2019) for processing, including quality filtering, adapter removal, and denoising (all code may be found at https://github.com/GemmaClucas/Matinicus-Rock-2021-Atlantic-Puffins/blob/main/MiFish_2022_Qiime_commands.Rmd and data is available at https://doi.org/10.6084/m9.figshare.28282811). Taxonomic assignments were made for the 12S region using an iterative blast method with a custom database downloaded from GenBank using the RESCRIPt plugin (Robeson et al., 2021), while a naïve Bayes classifier was used to classify the 18S sequences with the 99% clustered SILVA v.132 database (Quast et al., 2013). Using rarefaction curves, we determined that 2,500 sequences per sample were required for the 18S marker and 200 sequences per sample were required for 12S analyses. Samples were rarefied to these depths and all samples with an insufficient number of sequences were removed from our data set.

Taxonomic assignments of sequences were verified using the National Center for Biotechnology Information's (NCBI) BLAST tool (NCBI, 2023), and we used FishBase (Froese & Pauly, 2023) to check species' geographic distributions to ensure assignments were reasonable. Data from fecal DNA metabarcoding analyses were summarized using the frequency of occurrence (% of fecal samples in which a taxon occurred) and relative read abundance (% of DNA reads attributed to a taxon).

RESULTS

We collected 25 fecal samples from the RBTR roost site over two years (2020: *n* = 11, 2021: *n* = 14). Using the 12S gene, we amplified sufficient fish DNA from 16 of these samples for use in our analyses. We detected six different fish species in the RBTR's diet (Table 1), with ~75% of all fish DNA sequences attributable to just two species: Atlantic Saury *Scomberesox saurus* and Atlantic Mackerel *Scomber scombrus*. The high frequency of occurrence and high DNA relative read abundance from saury and mackerel (Fig. 2) suggest that these two species were the fishes consumed most commonly and in the greatest amount by the Seal Island RBTR. In contrast, analyses using 18S DNA were confounded by large quantities of amplified host (i.e., RBTR) DNA; removal of host DNA during processing left few samples with adequate read depth for diet analysis. However, the greatest proportion of recovered DNA came from teleost fish, suggesting these comprised the major component of the RBTR's diet during our study. All non-vertebrate taxa that we identified are likely attributable to parasites (e.g., nematodes), environmental contamination (e.g., fungi), or secondary ingestion (e.g., copepods), rather than direct consumption.

TABLE 1
Species identified using 12S primers in Red-billed Tropicbird *Phaethon aethereus* fecal samples collected in 2020 (*n* = 6) and 2021 (*n* = 10) from Seal Island, Maine, USA

Prey taxa	% FOO[a]		% Total reads[b]	
	2020	2021	2020	2021
Atlantic Herring *Clupea harengus*	33.3	0.0	33.3	0.0
Atlantic Mackerel *Scomber scombrus*	16.7	30.0	16.2	30.0
Atlantic Saury *Scomberesox saurus*	50.0	50.0	50.0	50.0
Fourbeard Rockling *Enchelyopus cimbrius*	16.7	0.0	0.3	0.0
Sandlance *Ammodytes* spp.	16.7	10.0	0.3	10.0
Silver Hake *Merluccius bilinearis*	0.0	10.0	0.0	10.0

[a] Percent frequency of occurrence (FOO) among samples
[b] Relative read abundance

DISCUSSION

Using molecular tools, we identified prey taxa consumed by a vagrant RBTR in two of the 17 years this individual was present at Seal Island, Maine. We identified six fish species present in the RBTR's diet, with Atlantic Mackerel and Atlantic Saury forming the majority of its diet, both in terms of frequency of occurrence and relative read abundance. DNA from fish prey were identified in most fecal samples examined, whereas we detected no DNA from likely invertebrate prey sources. Researchers noted a single squid beak at the RBTR roost site during sample collection (KCY, personal observation). However, such hard parts may persist for extended periods of time (Furness et al., 1984), so we were unable to determine if this was consumed during our study or not.

The species composition of the Seal Island RBTR's diet differed greatly from that reported in other published studies on RBTR diet. Most previous studies have sampled birds from breeding colonies at lower latitudes, and to our knowledge, none have documented RBTR consumption of any of the six fish species detected in this study. While dietary overlap is frequently described strictly in taxonomic terms, trait-based approaches can add valuable ecological context (Spitz et al., 2014).

The prey types consumed by the Seal Island RBTR have many physical and functional similarities to those consumed by RBTRs elsewhere. For instance, although two of the fish families most commonly consumed by RBTRs in the tropics—Exocoetidae (flyingfishes) and Belonidae (needlefishes)—are largely absent from the Gulf of Maine, the Seal Island RBTR fed heavily on fish taxa with similar lifestyles and body shapes (Castillo-Guerrero et al., 2011; Collette & Klein-MacPhee, 2002; Madden et al., 2022). These results suggest a preference for elongate, schooling fishes living near the sea surface in stratified, offshore waters. Moreover, these fishes are often driven to the surface by sub-surface predators, such as marine mammals or tuna, which RBTR in the tropics are known to forage in association with (Orta et al., 2020; Spear & Ainley, 2005). This combination of traits makes these prey taxa readily accessible to RBTRs, which are highly pelagic

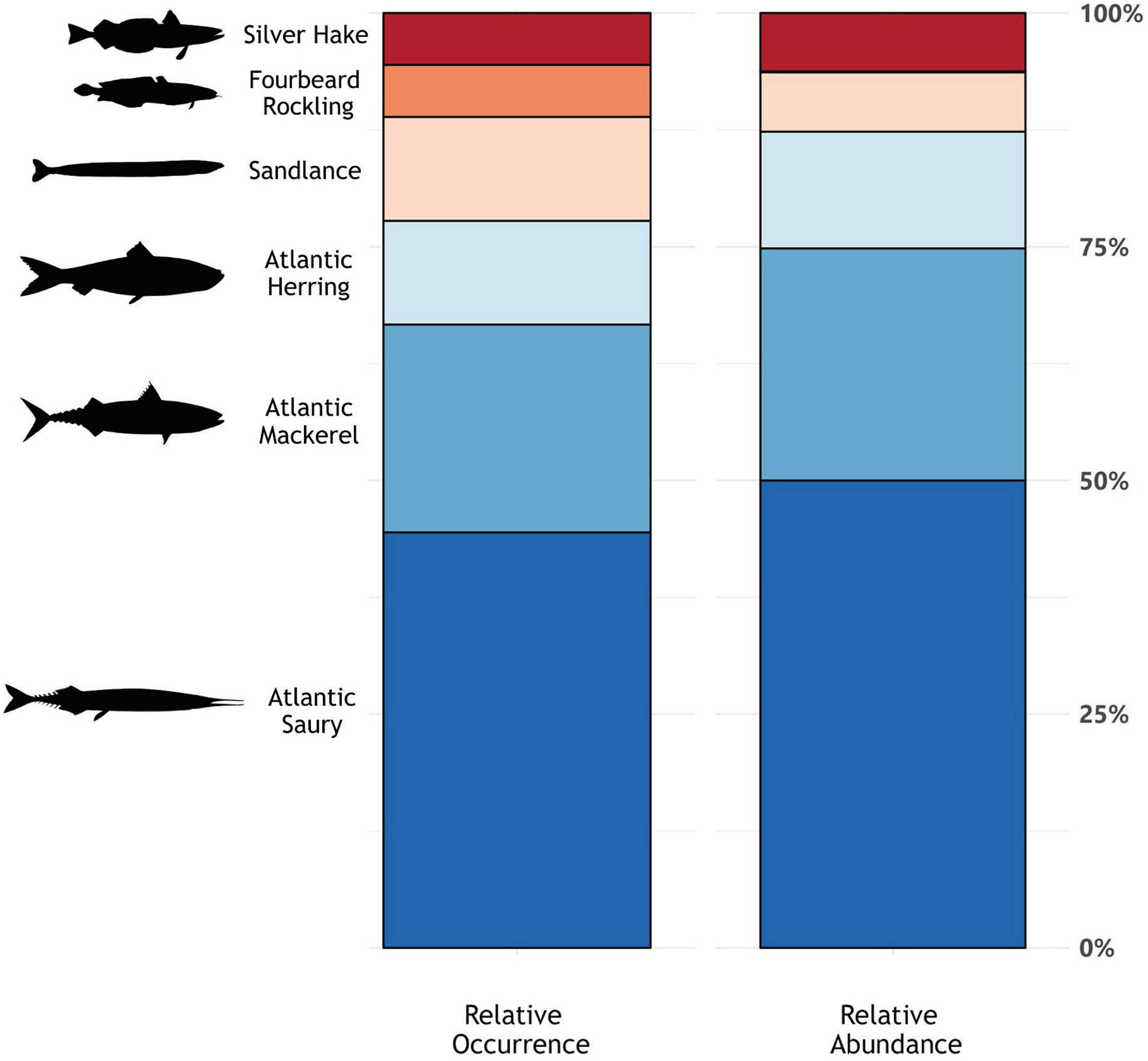

Fig. 2. Fish prey detected in Red-billed Tropicbird *Phaethon aethereus* fecal samples (*n* = 16), displayed as the relative frequency of occurrence and the relative abundance of DNA reads.

and capture prey during shallow plunge dives (Castillo-Guerrero et al., 2011). Although the prey targeted by the Seal Island RBTR may differ in species composition from prey that tropicbirds take elsewhere, many shared traits and functional similarities make saury and mackerel logical alternatives to traditional tropicbird prey.

Interestingly, saury and mackerel occur infrequently (typically ≤ 1%, by number) in the diets of Atlantic Puffins, terns, and other seabirds regularly monitored at Gulf of Maine colonies (Kress et al., 2016; Yakola et al., 2022; but see Kennerley et al., 2024). Therefore, we consider it likely that the RBTR was foraging in different areas than other Seal Island seabirds. In the Gulf of Maine, both saury and mackerel commonly feed in relatively warm, offshore waters (Collette & Klein-MacPhee, 2002; Radlinski et al., 2013), possibly beyond the more limited foraging ranges of chick-rearing terns and puffins. Notably, the Seal Island RBTR and Northern Gannets *Morus bassanus* in Newfoundland consumed many of the same prey species (Montevecchi, 2007), allowing us to speculate that these two pelagic plunge divers may have foraged in similar habitats, perhaps in association with subsurface predators. Remarkably, despite the RBTR's regular presence at Seal Island over many years, and frequent pelagic birding trips in the area, there are no recorded observations of the RBTR actively foraging, further suggesting that such behavior occurred far offshore.

As this study involved a single individual, the scope of inference is naturally very limited. Our sample collection began more than a decade after this individual was first documented in the Gulf of Maine, so we cannot determine how it initially reacted to its unfamiliar environment. We also acknowledge certain methodological limitations of our work. As in most metabarcoding studies, secondary ingestion—whereby the food items consumed by prey could be detected in a predator's feces—may have impacted our results. Larger size classes of Atlantic Mackerel prey on smaller fishes, and it is conceivable that some fish DNA in RBTR feces may be attributable to secondary ingestion. However, this is likely only the case for those taxa with comparatively low relative read abundance and is therefore unlikely to impact our identification of major prey types (Clucas et al., 2024; Kennerley et al., 2024).

Additionally, while all samples included in this study represent unique fecal deposits, prey DNA can persist in the digestive tracts of some seabirds for multiple days (Deagle et al., 2010). It is therefore possible that some prey DNA persisted in the RBTR's gastrointestinal system long enough to appear in multiple fecal deposits, meaning that our samples may not all be truly independent. These are valid concerns, although we believe any effects on our results were likely minimal, given the general similarity of the RBTR's diet across years.

Our results suggest that the Seal Island RBTR was capable of locating suitable prey resources despite major differences in the marine communities of the Gulf of Maine and the Caribbean. The regular occurrence of this individual over 17 consecutive years also suggests it was able to locate suitable prey consistently in the Gulf of Maine, despite significant environmental variability during this period (Balch et al., 2022). During our study, sea surface temperatures in one year (2021) were notably warmer than the other, breaking many regional records (Gulf of Maine Research Institute, 2021). We observed the absence of cold-adapted Atlantic Herring *Clupea harengus* (Rose, 2005) in the RBTR diet during the warmer year, yet saury and mackerel—more typical of warmer waters—occurred in both. This individual, therefore, was able to locate suitable prey during two years of variable ocean conditions. This is encouraging because many seabird populations will likely face changing prey communities due to climate change-mediated range shifts and the formation of no-analog marine communities (Pandolfi et al., 2020).

It is interesting to consider what would have happened had a suitable mate appeared at Seal Island at least once between 2005 and 2021. The apparent availability of suitable prey, along with the RBTR's regular occupation of a nest-like rock crevice, suggests that breeding may have been possible. While Veit (1988) argued that an environmental limiting factor (rather than limited dispersal ability) likely prevents RBTR from breeding in the Gulf of Maine, prey availability in this case did not appear to be a constraint. Ultimately, however, researchers on Seal Island never observed a second tropicbird, and the vagrant individual has not been observed since August 2021, eliminating the possibility of RBTR range expansion into the Gulf of Maine, at least for now. Nevertheless, our results demonstrate that RBTRs can successfully feed on novel prey types analogous to familiar ones, illustrating the adaptive potential of far-dispersing seabirds.

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AUTHOR CONTRIBUTIONS

WLK: Conceptualization, visualization, formal analysis, writing—original draft, writing—review & editing. GVC: Software, resources, methodology, investigation, formal analysis, writing—review & editing. DEL: Writing—review & editing, funding acquisition. KCY: Conceptualization, investigation, visualization, writing—review & editing.

REFERENCES

Balch, W. M., Drapeau, D. T., Bowler, B. C., Record, N. R., Bates, N. R., Pinkham, S., Garley, R., & Mitchell, C. (2022). Changing hydrographic, biogeochemical, and acidification properties in the Gulf of Maine as measured by the Gulf of Maine North Atlantic time series, GNATS, between 1998 and 2018. *Journal of Geophysical Research: Biogeosciences*, *127*(6), e2022JG006790. https://doi.org/10.1029/2022JG006790

Barbet-Massin, M., Thuiller, W., & Jiguet, F. (2012). The fate of European breeding birds under climate, land-use and dispersal scenarios. *Global Change Biology*, *18*(3), 881–890. https://doi.org/10.1111/j.1365-2486.2011.02552.x

Boeken, M. (2016). Breeding success of red-billed tropicbirds *Phaethon aethereus* on the Caribbean Island of Saba. *Ardea*, *104*(3), 263–271. https://doi.org/10.5253/arde.v104i3.a8

Bolyen, E., Rideout, J. R., Dillon, M. R., Bokulich, N. A., Abnet, C. C., Al-Ghalith, G. A., Alexander, H., Alm, E. J., Arumugam, M., Asnicar, F., Bai, Y., Bisanz, J. E., Bittinger, K., Brejnrod, A., Brislawn, C. J., Brown, C. T., Callahan, B. J., Caraballo-Rodríguez, A. M., Chase, J.,…Caporaso, J. G. (2019). Reproducible, interactive, scalable and extensible microbiome data science using QIIME 2. *Nature Biotechnology*, *37*(8), 852–857. https://doi.org/10.1038/s41587-019-0209-9

Buxton, R. T., Jones, C., Moller, H., & Towns, D. R. (2014). Drivers of seabird population recovery on New Zealand Islands after predator eradication. *Conservation Biology*, *28*(2), 333–344. https://doi.org/10.1111/cobi.12228

Castillo-Guerrero, J. A., Guevara-Medina, M. A., & Mellink, E. (2011). Breeding ecology of the Red-billed Tropicbird *Phaethon aethereus* under contrasting environmental conditions in the Gulf of California. *Ardea*, *99*(1), 61–71. https://doi.org/10.5253/078.099.0108

Clucas, G. V, Stillman, A., & Craig, E. C. (2024). From presence/absence to reliable prey proportions: A field test of dietary DNA for characterizing seabird diets. *BioRxiv*, 2024.03.22.586275. https://doi.org/10.1101/2024.03.22.586275

Collette, B. B., & Klein-MacPhee, G. (Eds.). (2002). *Bigelow and Schroeder's fishes of the Gulf of Maine* (3rd ed.). Smithsonian Institution Press. https://doi.org/10.22621/cfn.v117i2.711

Davis, R. A., & Watson, D. M. (2018). Vagrants as vanguards of range shifts in a dynamic world. *Biological Conservation*, *224*, 238–241. https://doi.org/10.1016/j.biocon.2018.06.006

Deagle, B. E., Chiaradia, A., McInnes, J., & Jarman, S. N. (2010). Pyrosequencing faecal DNA to determine diet of little penguins: Is what goes in what comes out? *Conservation Genetics*, *11*(5), 2039–2048. https://doi.org/10.1007/s10592-010-0096-6

Fayet, A. L., Clucas, G. V., Anker-Nilssen, T., Syposz, M., & Hansen, E. S. (2021). Local prey shortages drive foraging costs and breeding success in a declining seabird, the Atlantic puffin. *Journal of Animal Ecology*, *90*(5), 1152–1164. https://doi.org/10.1111/1365-2656.13442

Fjeldsa, J., Christidis, L., & Ericson, P. G. (2020). *The largest avian radiation: The evolution of perching birds, or the order passeriformes* (1st ed.). Lynx Editions. https://doi.org/10.1086/717382

Froese, R., & Pauly, D. (2023, February 23). *FishBase*. https://www.fishbase.org

Furness, B. L., Laugksch, R. C., & Duffy, D. C. (1984). Cephalopod beaks and studies of seabird diets. *The Auk*, *101*(3), 619–620. https://digitalcommons.usf.edu/auk/vol101/iss3/30

Grinnell, J. (1922). The Role of the "Accidental." *The Auk*, *39*(3), 373–380. https://digitalcommons.usf.edu/auk/vol39/iss3/7

Gulf of Maine Research Institute. (2021, October 26). *Gulf of Maine warming update: Summer 2021*. Gulf of Maine Research Institute. https://www.gmri.org/stories/gulf-of-maine-warming-update-summer-2021/

Henry, R. W., Shaffer, S. A., Antolos, M., Félix-Lizárraga, M., Foley, D. G., Hazen, E. L., Tremblay, Y., Costa, D. P., Tershy, B. R., & Croll, D. A. (2021). Successful long-distance breeding range expansion of a top marine predator. *Frontiers in Ecology and Evolution*, *9*, 620103. https://doi.org/10.3389/fevo.2021.620103

Kennerley, W. L., Clucas, G. V., & Lyons, D. E. (2024). Multiple methods of diet assessment reveal differences in Atlantic puffin diet between ages, breeding stages, and years. *Frontiers in Marine Science*, *11*. https://doi.org/10.3389/fmars.2024.1410805

Kress, S. W., Shannon, P., & O'Neal, C. (2016). Recent changes in the diet and survival of Atlantic puffin chicks in the face of climate change and commercial fishing in midcoast Maine, USA. *FACETS*, *1*(1), 27–43. https://doi.org/10.1139/facets-2015-0009

Lee, D. S., & Walsh-McGehee, M. (2000). Population estimates, conservation concerns, and management of Tropicbirds in the Western Atlantic. *Caribbean Journal of Science*, *36*(3–4), 267–279.

Lees, A. C., & Gilroy, J. J. (2014). Vagrancy fails to predict colonization of oceanic islands. *Global Ecology and Biogeography*, *23*(4), 405–413. https://doi.org/10.1111/geb.12129

Madden, H., Satgé, Y., Wilkinson, B., & Jodice, P. G. R. (2022). Foraging ecology of Red-billed Tropicbird *Phaethon aethereus* in the Caribbean during early chick rearing revealed by GPS tracking. *Marine Ornithology*, *50*(2), 165–175. http://doi.org/10.5038/2074-1235.50.2.1486

Maine Bird Records Committee. (2021). *Red-billed Tropicbird* (Phaethon aethereus). https://sites.google.com/site/mainebirdrecordscommittee/official-list-of-maine-birds/red-billed-tropicbird

McInnes, J. C., Alderman, R., Lea, M. A., Raymond, B., Deagle, B. E., Phillips, R. A., Stanworth, A., Thompson, D. R., Catry, P., Weimerskirch, H., Suazo, C. G., Gras, M., & Jarman, S. N. (2017). High occurrence of jellyfish predation by black-browed and Campbell albatross identified by DNA metabarcoding. *Molecular Ecology*, *26*(18), 4831–4845. https://doi.org/10.1111/mec.14245

Miya, M., Sato, Y., Fukunaga, T., Sado, T., Poulsen, J. Y., Sato, K., Minamoto, T., Yamamoto, S., Yamanaka, H., Araki, H., Kondoh, M., & Iwasaki, W. (2015). MiFish, set of universal PCR primers for metabarcoding DNA from fishes. *Royal Society Open Science*, *2*, 150088. https://doi.org/10.1098/rsos.150088

Montevecchi, W. A. (2007). Binary dietary responses of northern gannets *Sula bassana* indicate changing food web and oceanographic conditions. *Marine Ecology Progress Series*, *352*, 213–220. https://doi.org/10.3354/meps07075

Oro, D., Martínez-Abraín, A., Villuendas, E., Sarzo, B., Mínguez, E., Carda, J., & Genovart, M. (2011). Lessons from a failed translocation program with a seabird species: Determinants of success and conservation value. *Biological Conservation*, *144*(2), 851–858. https://doi.org/10.1016/j.biocon.2010.11.018

Orta, J., Jutglar, F., Garcia, E., & Kirwan, G. M. (2020). Red-billed Tropicbird (*Phaethon aethereus*), version 1.0. In J. del Hoyo, A. Elliott, J. Sargatal, D. Christie, & E. de Juana (Eds.), *Birds of the world*. Cornell Lab of Ornithology. https://doi.org/10.2173/bow.rebtro.01

Pandolfi, J. M., Staples, T. L., & Kiessling, W. (2020). Increased extinction in the emergence of novel ecological communities. *Science*, *370*, 220–222. https://doi.org/10.5281/zenodo.4031861

Quast, C., Pruesse, E., Yilmaz, P., Gerken, J., Schweer, T., Yarza, P., Peplies, J., & Glöckner, F. O. (2013). The SILVA ribosomal RNA gene database project: Improved data processing and web-based tools. *Nucleic Acids Research*, *41*(D1), D590–D596. https://doi.org/10.1093/nar/gks1219

Radlinski, M. K., Sundermeyer, M. A., Bisagni, J. J., & Cadrin, S. X. (2013). Spatial and temporal distribution of Atlantic mackerel (*Scomber scombrus*) along the northeast coast of the United States, 1985–1999. *ICES Journal of Marine Science*, *70*(6), 1151–1161. https://doi.org/10.1093/icesjms/fst029

Robeson, M. S., O'Rourke, D. R., Kaehler, B. D., Ziemski, M., Dillon, M. R., Foster, J. T., & Bokulich, N. A. (2021). RESCRIPt: Reproducible sequence taxonomy reference database management. *PLoS Computational Biology*, *17*(11). https://doi.org/10.1371/journal.pcbi.1009581

Rose, G. A. (2005). On distributional responses of North Atlantic fish to climate change. *ICES Journal of Marine Science*, *62*(7), 1360–1374. https://doi.org/10.1016/j.icesjms.2005.05.007

Spear, L. B., & Ainley, D. G. (2005). At-sea behaviour and habitat use by tropicbirds in the eastern Pacific. *Ibis*, *147*(2), 391–407. https://doi.org/10.1111/j.1474-919x.2005.00418.x

Spitz, J., Ridoux, V., & Brind'Amour, A. (2014). Let's go beyond taxonomy in diet description: Testing a trait-based approach to prey-predator relationships. *Journal of Animal Ecology*, *83*(5), 1137–1148. https://doi.org/10.1111/1365-2656.12218

Storey, A. S., & Lien, J. (1985). Development of the First North American colony of Manx Shearwaters. *The Auk*, *102*(2), 395–401. https://doi.org/10.2307/4086788

Thomas, C. D. (2010). Climate, climate change and range boundaries. *Diversity and Distributions*, *16*(3), 488–495. https://doi.org/10.1111/j.1472-4642.2010.00642.x

Veit, R. R. (1988). Why don't Red-billed Tropicbirds nest on Martha's Vineyard*? Bird Observer*, *16*(1), 11–16.

Veit, R. R. (1989). Vagrant birds: Passive or active dispersal? *Bird Observer*, *17*(1), 25–30. https://digitalcommons.usf.edu/bird_observer/vol17/iss1/7

Veit, R. R. (2000). Vagrants as the expanding fringe of a growing population. *The Auk*, *117*(1), 242–246. https://doi.org/10.1093/auk/117.1.242

Veit, R. R., Velarde, E., Horn, M. H., & Manne, L. L. (2021). Population growth and long-distance vagrancy leads to colonization of Europe by Elegant Terns *Thalasseus elegans*. *Frontiers in Ecology and Evolution*, *9*. https://doi.org/10.3389/fevo.2021.725614

Yakola, K., Jordaan, A., Kress, S., Shannon, P., & Staudinger, M. D. (2022). Interspecific and local variation in tern chick diets across nesting colonies in the Gulf of Maine. *Waterbirds*, *44*(4), 397–414. https://doi.org/10.1675/063.044.0402

Zawadzki, L. C., Veit, R. R., & Manne, L. L. (2019). The influence of population growth and wind on vagrancy in a North American passerine. *Ardea*, *107*(2), 131–147. https://doi.org/10.5253/arde.v107i2.a2