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Recent expansion of the Atlantic cownose ray (*Rhinoptera bonasus*) into Bermudian waters

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Cownose rays (Family Rhinopteridae) are highly migratory pelagic rays that are generally restricted to continental shelves. Despite 100's of years of natural history records, cownose rays have never been reported in Bermuda, an atoll-like coral reef ecosystem that is separated from the continental mainland United States by ~1,000 km. Here we compile evidence that the Atlantic cownose ray (*Rhinoptera bonasus*) has recently established in Bermuda, supported by both morphological and genetic data. Potential ecological and inter-specific competition concerns are presented as well as probable physical mechanisms that facilitated this recent and presumed range expansion.

KEYWORDS

elasmobranch, Bermuda, Atlantic, cownose, batoid, ray, range expansion, migration

1 Introduction

Situated in the northwest region of the Sargasso Sea, Bermuda comprises a group of oceanic islands and surrounding reefs that approximate an atoll formation (1). The islands are isolated from the North American continent (~1,000 km from Cape Hatteras, North Carolina) and are considered part of the tropical northwestern Atlantic ecoregion (2). However, at 32°N latitude, Bermuda supports the northernmost coral reef ecosystem in the Atlantic and is more accurately considered subtropical, characterized by significantly lower faunal and algal diversity than analogous ecosystems in the Greater Caribbean (3).

Research on elasmobranchs (i.e., sharks and batoids) in Bermuda has been modest, with a few studies of the sixgill shark (*Hexanchus griseus*) (4, 5), satellite tracking of the tiger shark (*Galeocerdo cuvier*) (6, 7), and the only research on batoids coming from a single species, the whitespotted eagle ray (*Aetobatus narinari*) (8–11). The whitespotted eagle ray has long been considered the sole inshore ray species in Bermuda (12); however, reports of large dasyatid rays (e.g., *Bathytosia centroura*) are emerging [(13); iNaturalist].

Cownose rays (family Rhinopteridae) are highly migratory pelagic stingrays that occur worldwide in tropical and temperate seas (14, 15). Currently, eight species have been identified in the sole genus *Rhinoptera*, including three in the North Atlantic basin—*R. bonasus* and *R. brasiliensis* [western Atlantic

species that are both Vulnerable on the International Union for Conservation of Nature (IUCN) Red List of Threatened Species (16, 17)], and *R. marginata* [a Critically Endangered eastern Atlantic species (18)]. To date, distribution patterns of these species have been limited to the continental shelf margins (16–18) with no reports from oceanic islands (Figure 1). Here, we report on the first observations of cownose rays in Bermuda, whose arrival is estimated to have occurred as early as 2012, with observations of the species continuing to be sustained through today.

2 Methods

We compiled recent information on cownose rays from Bermuda using multiple data sources: (1) informal, personal communications with Fisheries Officers and staff at the Bermuda Aquarium, Museum, and Zoo and Bermuda Institute of Ocean Sciences; (2) photographs contributed to Fisheries Officers by local citizen-scientists; and (3) recent on-water observations and collections conducted by the authors.

2.1 On-water observations and collections

Visual surveys were conducted by scientists in October 2022, July 2023, and October 2023. Surveys followed the methods of Ajemian et al. (8), targeting whitespotted eagle rays. Briefly, 2–3 individuals stood at the bow of the vessel while navigating across Harrington Sound and Flatts Inlet at slow speeds (<4 kt). When a ray was encountered, the position and time was recorded onto a handheld GPS unit (Garmin GPSMAP 78sc). Additional observations such as estimated group sizes and behaviors were also recorded.

Opportunistic collections of cownose rays by hand, seine, or entanglement nets were conducted by the Bermuda Aquarium, Museum, and Zoo in 2021 to acquire specimens for public display ($n = 2$) as well as by the authors herein during a single incidental encounter in October 2022 ($n = 3$). All rays were measured for disk width, weighed, and photographed. Additionally, to assign preliminary species identifications, tooth series counts were taken from the dorsal dental plate of the latter three individuals, following Jones et al. (19).

2.2 Genetic species identifications

Fin clips were collected and preserved in 70% ethanol from four cownose rays; one from an animal caught in 2021 that remains in captivity and three during the October 2022 surveys. Genomic DNA was extracted from ∼10–20 mg of each fin clip tissue with a Qiagen DNeasy™ DNA extraction kit (Qiagen, USA), using the manufacturer's protocol, except that tissue samples were digested for ∼12 h. A 442-base pair (bp) portion of the mitochondrial (mtDNA) NADH dehydrogenase subunit 2 (ND2) gene was amplified using a forward primer (5′-GAACCCYTTAATCCTCTYCATC-3′) by McDowell and Fisher (unpubl. data) and a reverse primer (5′-GGATTGATAGTACGCCTATGG-3′) by Weber et al. (20). Polymerase Chain Reaction (PCR) reactions and cycling conditions followed the methods described in Weber et al. (20). PCR products were cleaned using 3 μL of ExoSAP-IT (ThermoFisher) and sequenced by Eurofins Genomics, LLC (Louisville, KY) on an Applied Biosystems™ 3730XL DNA Analyzer with BigDye™ Terminator 3.1 sequencing chemistry (Applied Biosystems™). Forward and reverse sequences were aligned to create a consensus sequence for each individual in CodonCode v. 6.0.2 (CodonCode Corporation, Dedham, USA). Species identifications were verified via a NCBI Blast search that compared resultant haplotypes to known mtDNA ND2 haplotypes for cownose rays in the north Atlantic basin.

3 Results

3.1 Occurrence and distribution

Local entities recollect cownose ray presence in Bermuda as early as 2012, and they have since been observed across most of the island's protected coastal waters but not on the exposed South Shore (Figure 2, C.T. Flook, Bermuda Institute of Ocean Sciences, personal communication, October 2023). However, the first available photographic evidence of cownose rays was obtained from an encounter on 12 May 2016 by a citizen scientist. These photographs were taken at Mill Creek in the parish of Pembroke, and although only two individuals were photographed swimming together (Figure 3), school sizes of up to 12 individuals were reported from the adjacent Great Sound within months of that sighting (M. Jones, personal communication, May 2016). Recent on-water surveys revealed 14 individual sightings of cownose rays in the Flatt's Inlet—Harrington Sound region of Bermuda between October 2022 and 2023 (Figure 2). Sightings included group sizes ranging from 1 to 12 individuals, with the largest groups observed in Flatt's Inlet and smaller groups (1–2 individuals) in the southern and western portions of Harrington Sound.

3.2 Collections

A total of five individual cownose rays were collected between 2021 and 2022. All individuals collected were females, and thus maturity state could not be assessed based on external anatomy. The first two individuals (CNR-1 and CNR-2) were captured as sole individuals in Harrington Sound while the three individuals collected in 18-Oct 2022 (CNR-3,4, and 5) were part of a school size estimated at 12 individuals in Flatts Inlet (Figure 3).

3.3 Species identifications

Tooth series counts for the three individuals collected in October 2022 were all 7, suggesting the captured species was *R. bonasus* (Table 1). Genetic analysis for the fin clips from four cownose rays revealed two mtDNA ND2 haplotypes that matched known haplotypes for *R. bonasus*, with only a single bp mutation between the two haplotypes. The haplotype for the single animal

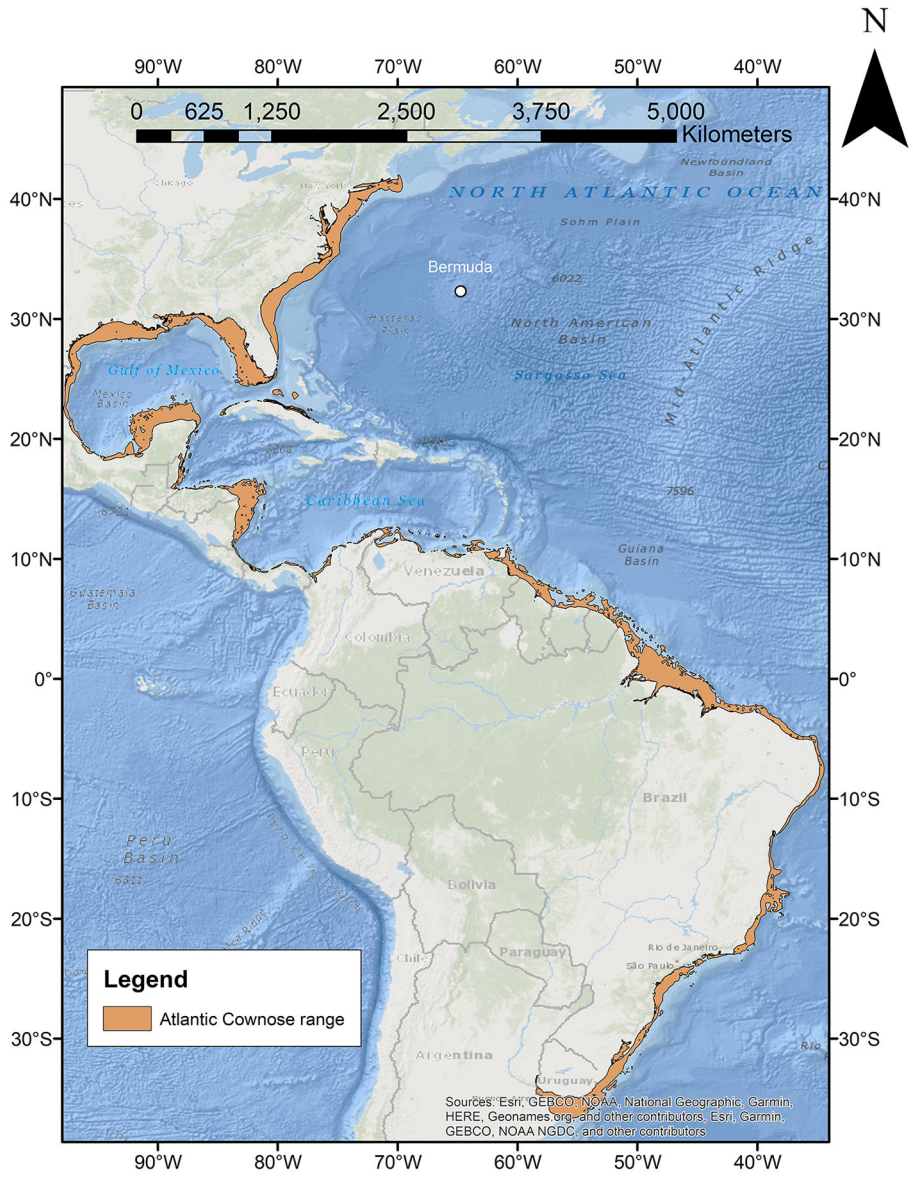

FIGURE 1
Map of current *R. bonasus* distribution (orange polygons) as per Carlson et al. (16) in relation to Bermuda (white circle).

caught in 2011 (CNR-2) matched 100% with RBON16 (GenBank accession no. MT410202), whereas the haplotypes for the three individuals caught in the October 2022 surveys (CNR-3-5) were 100% similar to RBON1 (GenBank accession no. MT410194) [see Weber et al. (20)].

4 Discussion

4.1 Species identification

The combination of morphological and genetic data support the species identification of *R. bonasus*. Tooth column counts do not match identifications for congeneric species in the Atlantic, *R. brasiliensis* or *R. marginata*, both of which are reported to have 13 series (21). The two mtDNA ND2 haplotypes from the four individuals were a 100% match to known *R. bonasus* haplotypes. RBON1, found in three individuals, is a common haplotype previously found in individuals from the east coast of the U.S. and the northeastern Gulf of Mexico [see Weber et al. (20)]. RBON16, seen here in one individual, was previously only found in a single individual from the east coast of the U.S. (20). These haplotypes are 5.66–5.88% different to known *R. brasiliensis* mtDNA ND2 haplotypes [see Weber et al. (20)], making it unlikely the Bermuda specimens are *R. brasiliensis*. While the possibility that these individuals are hybrids cannot be ruled out since mtDNA is maternally inherited, hybridization of cownose rays in the wild has not been documented.

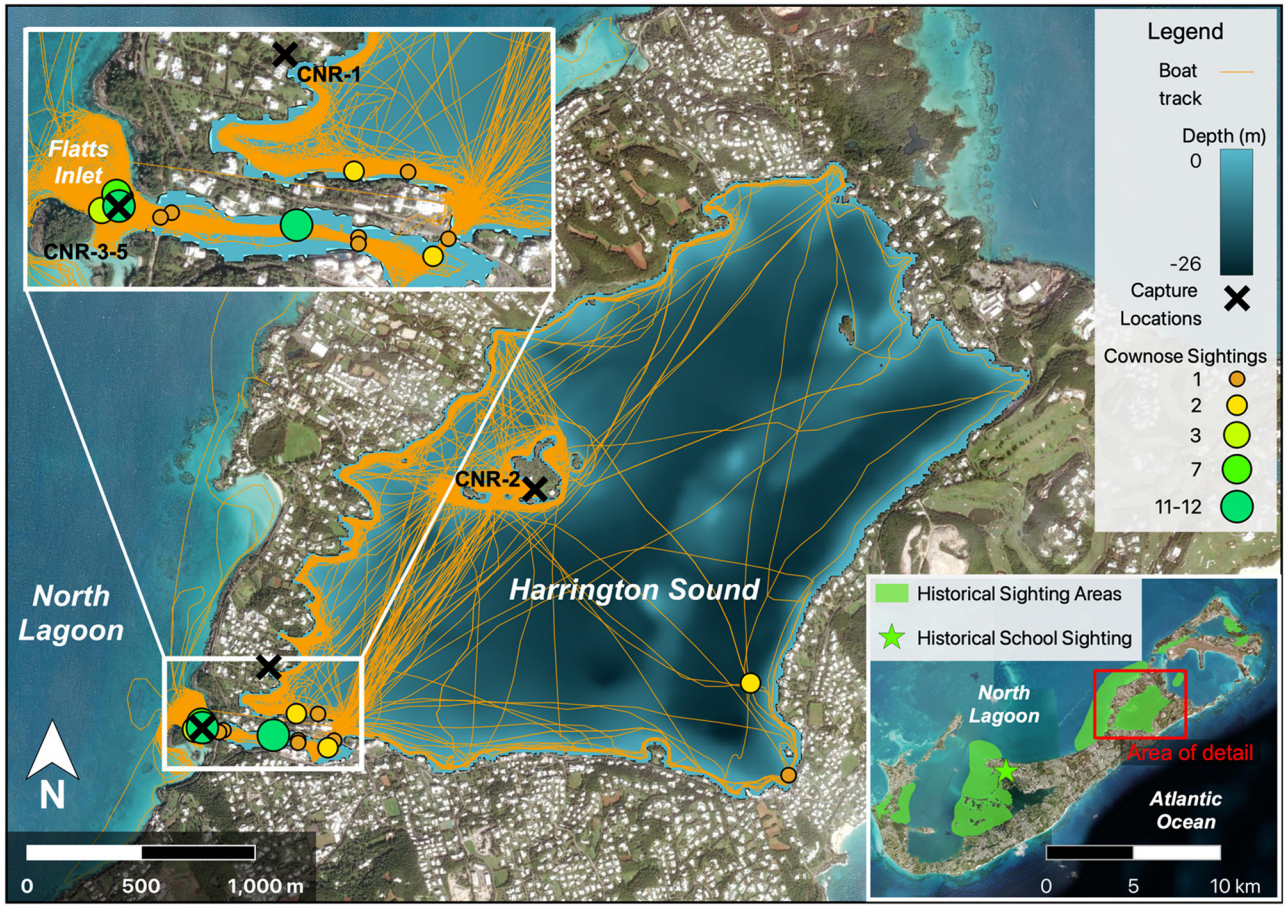

FIGURE 2
Map of cownose ray sightings across Bermuda. Inset map **(bottom right)** represents the overview of Bermuda and all regions where cownose rays have been reported (green polygon), with the green star marking Mill Creek where photographs were obtained from 2016 (Figure 3). Red box bounds the Harrington Sound and Flatts Inlet region, which is expanded in detail on the left **(top-left)** and displays sighting locations and estimated school sizes from 2021 to 2023, overlain atop vessel tracks (orange polylines) and bathymetry of Harrington Sound. Black "X" marks capture location of rays collected in 2021 and 2022.

4.2 Range expansion of the Atlantic cownose ray

Research on *R. bonasus* occurrence and migratory patterns in the Greater Caribbean region (including the Caribbean Sea, Gulf of Mexico, Bahamas, Bermuda, and the Florida peninsula) is sparse outside of continental U.S. and Mexican waters. To date, compiled data suggest the species broadly extends across the Atlantic coastlines of the South and Central American continents (16). As such, the recent finding of cownose rays in Bermuda, after hundreds of years of natural history records, suggests this is a novel species range expansion to this atoll-like system.

It is currently unknown whether *R. bonasus* in Bermuda is resident or seasonally migratory. Based on thermal conditions alone, cownose rays can likely reside in Bermuda for extended periods. Outmigration of cownose rays along the Atlantic coast (i.e., southbound departure from the Chesapeake Bay in fall) is triggered by changes in thermal conditions; in particular, as temperatures fall below 20°C (22, 23). In Bermuda, wintertime temperatures can approach 15°C within shallow inshore bays (1), which could force rays to become migratory. However, since those conditions do not last for long periods, it is possible rays simply move to warmer waters in the North Lagoon, similar to the pattern observed in the northern Gulf of Mexico (9, 24), or are resident, as reported in parts of south Florida (25, 26). Along the Atlantic coast of the U.S., northward migration cues for females and males depend on different factors: sea surface temperature for females, and day of year for males (22). While all collections of cownose rays in Bermuda to date are of females, the acquisition of small, immature rays (e.g., CNR-3) suggests pupping may have recently occurred here. Moreover, there have been reports of behaviors approximating copulation (C. Aming, personal communication, July 2023), including close-following and biting of pectoral fins as described by McCallister et al. (10), suggesting that male rays are also present in the area. Should cownose rays continue to survive in Bermuda waters, the species' low fecundity (1 pup/year) will limit its capacity for rapid population growth (16). However, a more accurate assessment of the current population size is sorely needed.

FIGURE 3
Photograph of cownose rays in Mill Creek, Bermuda on 12 May 2016 (credit: M. Jones).

4.3 Potential mechanisms of dispersion

While Bermuda is (at its closest) 960 km from Cape Hatteras, North Carolina, and thus within the migration distances (<1,000 km) recorded for cownose rays along the continental U.S. (27, 28), movements over deep ocean basins (i.e., off the continental shelf) appear uncommon [max recorded depth ~50 m (27)]. Though capable of extensive migrations (100's of km) in the Gulf of Mexico (29), the native and related pelagic ray species *A. narinari* does not appear to leave Bermuda waters seasonally (8, 9), although movements into deeper waters are likely in the winter (11). The tiger shark, on the other hand, regularly migrates between Bermuda, Bahamas, and the Turks and Caicos Islands (6), Lemon (*Negaprion brevirostris*) and blacktip (*Carcharhinus limbatus*) sharks are capable of similar migrations over deep waters and have also been recorded to connect waters of the U.S. Virgin Islands and Florida Atlantic coast (30). As a benthic mesopredator, such an offshore migration would be energetically expensive and potentially risky for cownose rays, suggesting that physical (i.e., abiotic) forcing facilitated the species' dispersion.

Oceanography may have played a major role in this founder dispersal event for *R. bonasus*, as oceanic currents significantly influence the trajectory of migrating marine animals (31, 32). Often interacting with oceanography are atmospheric conditions such as windage and extreme weather events (e.g., storms), which have been shown to trigger abnormal migratory behaviors in other large marine taxa such as loggerhead sea turtles (*Caretta caretta*) (33). Interestingly, during the time period preceding the expansion of cownose rays to Bermuda (i.e., winter 2010), the North Atlantic Ocean experienced a pronounced southward shift in westerly winds that were also unusually strong and influenced current dynamics in the region (34). This transition, fueled by anomalously negative North Atlantic Oscillation Indices in winter 2009–2010, December 2010, and March 2013, narrowed a normally larger convergence zone in the Sargasso Sea and facilitated unprecedented advection of floating *Sargassum* seaweed toward the eastern Atlantic (34), including Bermuda (S.R. Smith, pers. obs). This climatological anomaly and associated oceanographic changes may have played a similar role in shifting pelagic cownose rays eastward from their established range. Indeed, a single cownose ray that was satellite tagged in Chesapeake Bay in October 2009 and moved southward off the Carolinas in November was apparently geolocated in the Gulf Stream at the end of its track in January 2010 (27), suggesting potential temporal alignment with these conditions. This movement pattern was considered unusual for rays tagged in Chesapeake Bay, which are otherwise located off central Florida's Atlantic coast during wintertime (27, 28). Unfortunately, information on other tagged individuals was not available from this same period, restricting our interpretation of this basin-scale event as the sole mechanism behind cownose ray dispersion.

Extensive tropical storm activity also occurred between Bermuda and the continental U.S. in the years leading up to the first purported cownose ray sightings (http://coast.noaa.gov/hurricanes), including storms that could have interacted with southward migrating cownose rays in fall (e.g., Hurricane Sandy, October 2012) and displaced these animals offshore into the Gulf Stream. Similar events may have also played a role in re-distributing other benthic ray species recently sighted in Bermuda such as *B. centroura* (13), although this stingray is known to inhabit much deeper waters (35) and could possibly have gone unnoticed until recently. In summary, it is possible that multiple oceanographic changes and weather events facilitated cownose ray arrival to Bermuda.

4.4 Ecological considerations

Cownose rays have likely been in Bermuda for a decade already. This presents an interesting set of potential interactions with an otherwise stable subtropical marine ecosystem. One concern is related to the locally protected *A. narinari*, which is a native resident of Bermuda (12). Rays of the genera *Rhinoptera* and *Aetobatus* overlap in habitat and trophic niche elsewhere in subtropical to warm temperate waters around the globe. Due to the presence of mollusks in both species' diet, fishermen in the Mexican Gulf have expressed concern over competition between the two species and even suspected cownose rays negatively impact the more valuable eagle rays, which are fished locally (36). However, recent dietary data suggest the two species exhibit only modest niche overlap (37). A recent isotopic study suggested *Aetobatus* is less trophically constrained than *Rhinoptera*, possibly due to its larger size, gape, and buccal morphology, allowing it to exploit a wider range of prey (38). In Florida's Indian River Lagoon, the two genera occupy similar spaces, although visitation patterns to the same habitats are asynchronous (26). Additionally, cownose rays appear more associated with estuaries and can tolerate considerably lower salinities than *A. narinari* (24, 39), although these conditions are uncommon in Bermuda. Mill Creek, where the first confirmed (via photographs) encounter of *R. bonasus* occurred, is the only true estuary in Bermuda (40) and is lined with red and black mangroves and adjoining marsh land (41). Thus, while cownose rays have clearly expanded to other parts of Bermuda, this affinity for areas

TABLE 1 Biological and genetic characteristics of the five individual cownose rays collected and analyzed in the study.

ID	Date	Sex	Disk width (cm)	Disk length (cm)	Total length (cm)	Weight (kg)	Tooth series count	Fin clip taken?	mtDNA ND_2 haplotype/ GenBank accession no.
CNR-1	9-Mar-2021	Female	69.5	45.0	–	4.6	–	N	–
CNR-2	13-Jul-2021	Female	100.0	66.0	–	13.5	–	Y	RBON16/MT410202
CNR-3	18-Oct-2022	Female	57.0	34.0	37.4	4.1	7	Y	RBON1/MT410194
CNR-4	18-Oct-2022	Female	68.9	42.0	46.1	6.8	7	Y	RBON1/MT410194
CNR-5	18-Oct-2022	Female	83.0	50.8	53.6	10.0	7	Y	RBON1/MT410194

influenced by freshwater may partition them away from habitats occupied by eagle rays, and limit competition between the species.

4.5 Research needs

Several basic questions regarding cownose rays need to be addressed to understand their potential to interact with native species and resources, as well as how the species may fare in Bermuda in the future. The first is a question of how many cownose rays are actually present in Bermuda. At the moment, it remains unclear as to whether there is a single group of cownose rays that is repeatedly re-sighted in various locations, or whether the species is more broadly distributed across inshore sounds and harbors. This information could be gleaned using systematic aerial surveys, which has been successful elsewhere in documenting cownose ray distribution and extent (24, 42–44). Additionally, monitoring of size-class data may help to determine the level of reproductive success of the established population. Next, dietary information should be obtained from cownose rays to identify the prey resources that the species is interacting with, and whether any of these are shared with the protected *A. narinari*. Lastly, more research should be conducted into the potential mechanisms that facilitated the arrival of cownose rays to Bermuda, as this could reveal whether additional introductions of this species (and others) are possible in the future.

Data availability statement

The datasets presented in this study can be found in online repositories. The names of the repository/repositories and accession number(s) can be found in the article/supplementary material.

Ethics statement

The animal study was approved by Institutional Animal Care and Use Committee, Florida Atlantic University. The study was conducted in accordance with the local legislation and institutional requirements.

Author contributions

MA: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing. CH: Data curation, Formal analysis, Investigation, Methodology, Software, Visualization, Writing – original draft, Writing – review & editing. LC: Data curation, Formal analysis, Investigation, Methodology, Writing – original draft, Writing – review & editing. JP: Conceptualization, Data curation, Investigation, Project administration, Resources, Writing – original draft, Writing – review & editing. SS: Conceptualization, Data curation, Investigation, Methodology, Project administration, Resources, Writing – original draft, Writing – review & editing. CJ: Conceptualization, Data curation, Methodology, Resources, Writing – original draft, Writing – review & editing. NP: Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Supervision, Writing – original draft, Writing – review & editing.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

The first author declared that he was an editorial board member of Frontiers, at the time of submission. This had no impact on the peer review process and the final decision.

Publisher's note

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