CARIBBEAN AUDUBON'S SHEARWATERS *PUFFINUS LHERMINIERI* CHOOSE NESTING LOCATIONS THAT IMPROVE MALE AND FEMALE PRE-LAYING EXODUS FORAGING STRATEGIES

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ABSTRACT

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This study aims to better understand how the nesting distribution of Audubon's Shearwaters *Puffinus lherminieri* in the Caribbean is associated with the location of predictable ocean fronts, in turn reflecting the different foraging strategies employed by males and females during their pre-laying exodus. The study compares the spatial distribution of bathymetric features — generators of fronts — relative to the pre-laying exodus foraging areas of male and female shearwaters in 89 known nesting locations and in a control group of 5 621 remaining islands in the Caribbean. For each location, the density of potential locations within the foraging radius of males (270 km) and females (270–850 km) was calculated by geographic information system (GIS) analysis. Foraging sites for males tended to be more densely aggregated and those for females less densely aggregated when compared with the controls, but, for both, a correlation between the proximity of nesting locations and likely frontal regions was clear. These data indicate that nesting locations appear to be associated with predictable thermal fronts. This strategy improves the shearwaters' access to food sources during the pre-laying exodus.

Key words: Audubon's Shearwater, pre-laying exodus, Caribbean, foraging areas, fronts, bathymetry

INTRODUCTION

The Audubon's Shearwater *Puffinus lherminieri* is a small seabird with a pantropical distribution. An estimated 3 000–5 000 shearwater pairs currently nest in the Caribbean, representing a decline in numbers from the beginning of the 20th century (BirdLife 2008, Schreiber & Lee 2002). Included in the Caribbean population are subspecies *P. l. lherminieri* and the nearly extinct *P. l. loyemilleri* (Balloffet *et al.* 2006). Work related to understanding the spatial distribution of these subspecies' breeding sites has been limited. Research on the Caribbean populations of this species has been confined primarily to studies of their ecology at single colonies within the Bahamas (Mackin 2004, Trimm 2004). Understanding the factors that affect the spatial selection of nest locations can aid future conservation efforts by providing clues about where to locate colonies without the need for large-scale surveys.

Reliable ocean fronts, which are driven by bathymetric features, strongly predict seabird foraging locations (Hyrenbach *et al.* 2000). Zooplankton-rich mesoscale fronts form near ocean trenches, seamounts, and sharp changes in subsurface terrain (Valavanis *et al.* 2005). These fronts, often detectable because of abrupt changes in sea surface temperature, are derived from ocean processes related to subsea topography and, thus, are highly predictable (Nur *et al.* 2011, Wolanski & Hamner 1988). Fronts, therefore, represent reliable foraging grounds for seabirds, as prey species predictably congregate to feed on the abundant zooplankton in these areas (Reese *et al.* 2011). Potential nesting locations for Audubon's Shearwater in the Caribbean and off the coast of Brazil have recently been predicted by bathymetry, along with several other oceanographic variables (Chatfield-Taylor 2015, Lopes *et al.* 2014). Food-rich areas, such as fronts, are the primary destination for females during the pre-laying exodus, when females acquire the energy and nutrients needed to form eggs (Perrins & Brooke 1976, Werner *et al.* 2014). There have been no studies of the pre-laying exodus of Audubon's Shearwater (Warham 1990). However, behavior of the closely related Manx Shearwater *P. puffinus* may be used to predict the pre-laying exodus of Audubon's Shearwater (A.J. Delnevo, pers. comm.).

Unlike many shearwater species, the male Manx Shearwater does not participate in the exodus (Brooke 1990), likely true of Audubon's Shearwaters as well. Indeed, both Manx and Audubon's shearwaters breed asynchronously, requiring the male to return nightly to the nesting site to guard its burrow from later-nesting pairs (Brooke 1990, Trimm 2004). Studies of Cory's Shearwaters *Calonectris diomedea* show that nest-guarding behavior leads males to forage significantly closer to the nest than females during the pre-laying exodus (Werner *et al.* 2014). Hence, during the pre-laying exodus, female Manx Shearwaters forage at greater distances than males; the sexes' foraging areas do not overlap, reducing competition for resources (Brooke 1990). The female foraging area, therefore, surrounds the roughly circular foraging area of males; its radius is known from individuals from Welsh colonies recovered in the Bay of Biscay 850 km away (Perrins & Brooke 1976). Estimates of the male foraging radius are known from tracking studies conducted by Guilford *et al.* 2009. The distinctly different foraging strategies and ecological roles of males and females suggest that the spatial distribution of areas of enhanced forage availability, therefore, could be an important factor in determining where nesting locations are established. This paper tests the hypothesis that the spatial distribution of Audubon's Shearwater nesting locations in the Caribbean is strongly affected by access to adjacent areas of enhanced feeding opportunities (i.e., fronts associated with bathymetric features), reflecting the foraging strategies of both sexes during the pre-laying exodus.

STUDY AREA AND METHODS

Bird observational data and selection

Eighty-nine known nesting locations (at least one recorded nest, as distinct from colonies) for Audubon's Shearwater in the Caribbean were georeferenced using geographic information systems (GIS; Fig. 1). The data were taken from Bradley & Norton (2009), Bright *et al.* (2014), A.J. Delnevo (pers. comm.), Dinsmore (1972), Hodge (2011), and Levesque & Yésou (2005). The primary dataset available for nesting seabirds in the Caribbean contains sampling bias, making it unsuitable as a source of control data (Bradley & Norton 2009). To avoid complications arising from using sample means from a non-random dataset, a control dataset consisting of the 5621 remaining islands in the Caribbean was used. This represents all available data, and the summary statistics derived are the population mean and standard deviation (SD), rather than a sample mean and SD.

The islands contained in this dataset include those with and without large human populations and those with or without populations of terrestrial predators. While detrimental, the presence of humans and terrestrial predators apparently does not preclude Audubon's Shearwaters from forming successful colonies. Several large colonies coexist with both humans and large predator populations (Bretagnolle *et al.* 2000, Chatfield-Taylor & Delnevo 2014). Points were calculated in the geometric center of the islands in the control dataset or were hand-digitized when this point fell outside the perimeter of the island. All data were manipulated in ArcGIS 10.1 (ESRI ArcMap 10.1). The spatial extent of the study area is approximately 98°W to 45°W, 40°N to 5°S.

Bathymetric breaks

Bathymetric data were obtained from the General Bathymetric Chart of the Oceans (GEBCO; GEBCO 2014), which has a spatial resolution of 30 arc-seconds. The author developed an algorithm using Python (Python Language Reference, version 2.7.5, Python Software Foundation) to locate sharp changes in bathymetry, which are referred to throughout this paper as "bathymetric breaks" (modified from Chatfield-Taylor 2015). Bathymetric breaks approximate a dense convergence of isobaths in a small geographic area, resulting in a sharp change in ocean topography. Only near-surface breaks were included in the analysis, as these areas are more likely to be associated with surface front formation, often indicated by abrupt changes in sea surface temperature (i.e., thermal fronts; Hoefer 2000); thus, bathymetric breaks having a bottom depth of more than 228.6 m (750 feet) were removed. The algorithm searches each cell in the GEBCO raster for all locations where there was a bathymetric change of at least 152.4 m (500 feet) between

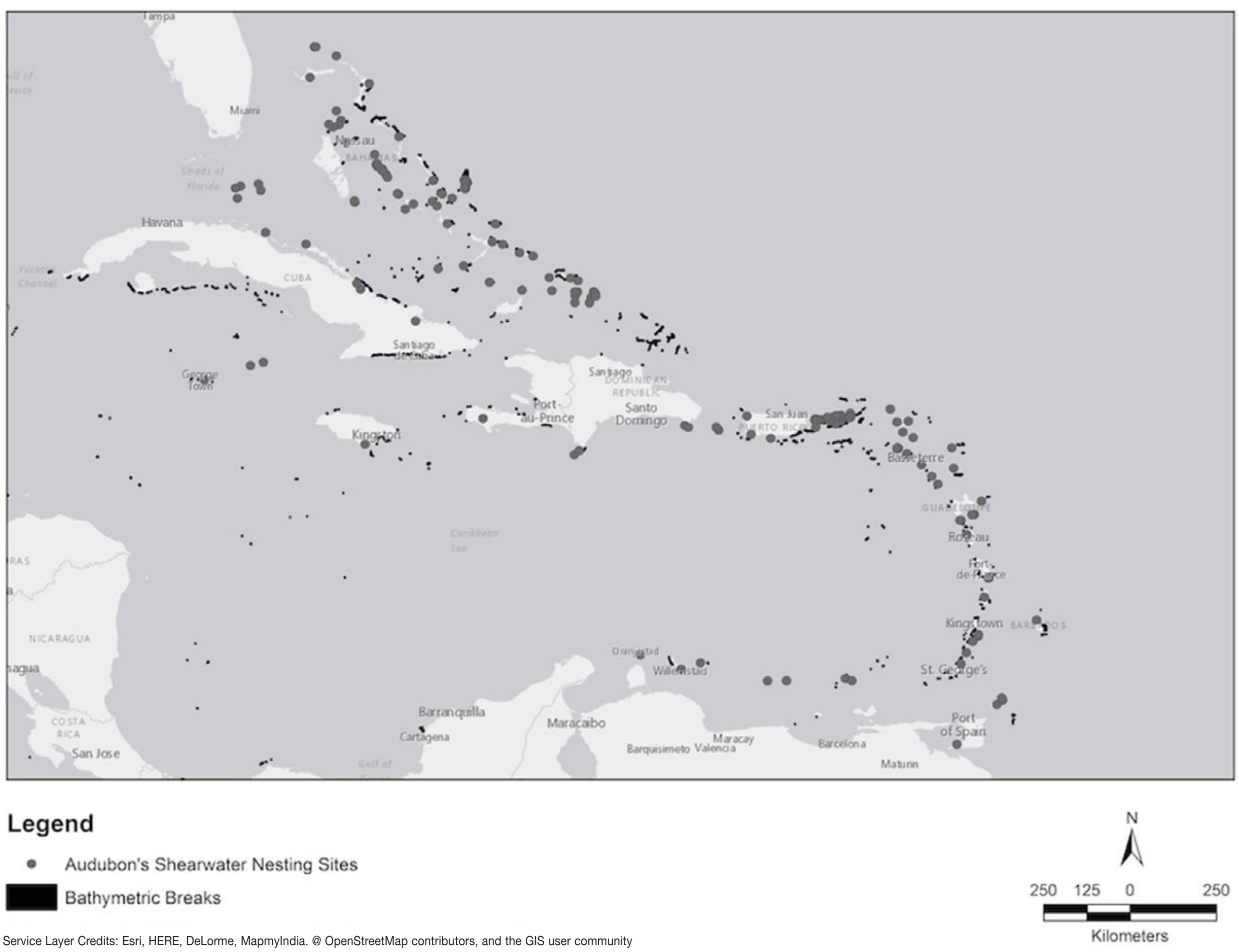

Fig 1. Map showing the distribution of Audubon's Shearwater nesting sites and the distribution of bathymetric breaks within the Caribbean.

the target cell and any of its eight neighbor cells. The output is a shapefile that can be converted to raster format. This dataset was verified for accuracy using ArcGIS.

Pre-laying exodus foraging ranges

Assumptions regarding the behavior of Audubon's Shearwater during its pre-laying exodus are based on the ecologically similar Manx Shearwater (A.J. Delnevo, pers. comm.). Perrins & Brooke (1976) recorded female Manx Shearwaters 850 km away from their colonies during their pre-laying exodus. This 850 km distance was used as the outer radius of the annulus-shaped female foraging area (zone of analysis) analyzed in this study. Males visit their burrows at night, requiring them to stay relatively close (Brooke 1990). Guilford *et al.* (2009) used global positioning system (GPS) monitoring to track male Manx Shearwaters during the pre-laying exodus and found that they ranged from immediately offshore to approximately 400 km. For this study, a male foraging distance of 270 km was assumed, given a maximum six-hour flight time each direction and the 45 km/h flight speed of a Manx Shearwater (Brooke 1990). This distance formed the radius for the male circular-shaped zone of analysis and the inner radius of the females' annulus-shaped zone.

Analysis and statistics

Data analysis was performed using the Spatial Analysis extension for ArcGIS 10.1. A raster variant of the bathymetric break dataset were created for use with the Focal Statistics function. Each bathymetric break was assigned a unique value, and missing data were assigned a value of zero. This raster was used as the input for the Focal Statistics "Variety" function. Focal Variety counts the number of uniquely valued raster elements within the focal window. With each bathymetric break assigned a distinct value, the result is the total number of breaks. The output is a raster with each cell assigned a value for the number of bathymetric breaks within the area of the focal window centered on that cell. The focal window size is based on cell numbers rather than linear distance, which necessitates calculating the number of cells in the raster being analyzed — equivalent to 270 km (294 cells) for males and 850 km (922 cells) for females. The male zone used a circular focal window and the female zone used an annulus.

Focal Variety was used to analyze the male and female zones of analysis, resulting in two rasters. Data were extracted from each raster by using the "Extract Values to Points" function. Using the two datasets as the input, this function extracted the raster values at each point in the dataset. This was the purpose behind using Focal Statistics; the raster format allows for data extraction anywhere within the extent of the raster. The data extraction created four shapefiles, and the data from these shapefiles were exported to Microsoft Excel (Microsoft Office Professional Plus version 14.0.7) for statistical analysis.

The density of bathymetric breaks was calculated by dividing the number of breaks within each zone by its area. The mean of the density was compared between the nesting and control datasets for both the male and female zones. The data for the male and female zones were then merged to form a single circular zone of analysis with a radius of 850 km. The mean bathymetric break density for this 850 km zone was compared between the nesting and control datasets. The densities of male and female zones from the nesting dataset were also compared. Two types of statistical tests were performed for each comparison: an F-test to test for equal variances, and either a Welch's t-test for unequal variances or a two-sample t-test for equal variances. Descriptive statistics are reported as the mean ± standard error.

RESULTS

In the male zone of analysis, the mean of the density of bathymetric breaks was significantly greater in the nesting dataset compared with the control dataset. The mean density (in breaks per square kilometer) of the male zone in the nesting dataset (0.000426 ± 0.000019, n = 89) was 131% of the mean for the control dataset (0.000324 ± 0.0000021, n = 5 621; Welch's t-test: $t_{90} = 5.3$, $P < 0.001$). In the female zone of analysis, the mean of the density of bathymetric breaks was significantly less in the nesting dataset compared with the control. The mean density of the female zone in the nesting dataset (0.000137 ± 0.0000035, n = 89) was 90% of the mean for the control dataset (0.000153 ± 0.00000057, n = 5 621; Welch's t-test: $t_{93} = -4.4$, $P < 0.001$).

When the two zones of analysis were merged, the difference in means of the density of bathymetric breaks was not significantly different between the nesting and control datasets. The mean density for the nesting dataset (0.000167 ± 0.0000036, n = 89) is 98% of the mean for the control dataset (0.00017 ± 0.00000057, n = 5 621; Welch's t-test: $t_{92} = -1.0$, $P = 0.31$). When the male and female zones for the nesting dataset were compared, the density of bathymetric breaks within the male zone was significantly different from that in the female zone (two-sample t-test: $t_{176} = -14.9$, $P < 0.001$).

DISCUSSION

The spatial distribution of bathymetric breaks relative to the pre-laying exodus foraging areas of male and female Audubon's Shearwaters was compared between 89 known nesting locations and the 5 621 remaining islands in the Caribbean. These bathymetric breaks are likely to be areas of high prey availability, as the conditions are appropriate for the formation of mesoscale thermal fronts that concentrate prey species (Wolanski & Hamner 1988, Hyrenbach *et al.* 2000, Nur *et al.* 2011, Valavanis *et al.* 2005). Reliable foraging locations are of particular importance during the pre-laying exodus to allow males and females to fulfill their respective roles of nest-guarding and egg formation (Brooke 1990, Warham 1990). The nest-site fidelity exhibited by Audubon's Shearwaters suggests that these static features can be visited in successive years once identified, an aspect important to seabirds (Nur *et al.* 2011, Trimm 2004).

This study found an association between the distribution of nesting locations and differing foraging location densities for male and female Audubon's Shearwaters, considering both islands with and without significant anthropogenic factors. Males are associated with areas having a high density of foraging locations, allowing them to increase feeding time while staying close enough to guard their nests. Females are associated with significantly less dense foraging area, both compared with males and compared with the Caribbean mean, indicating that, within their foraging range, prey can be densely concentrated at a small number of locations. Female shearwaters thus may concentrate on a few resource-rich areas, a strategy that improves foraging efficiency by eliminating excessive flight between larger numbers of relatively resource-poor areas.

When examined in relation to the rest of the Caribbean, the distribution of Audubon's Shearwater nesting locations improves the effectiveness of both sexes' foraging strategies during the pre-laying exodus. I suggest that there is a direct causal relationship between the distribution of static, predictable food resources, as they relate to the sexes' pre-laying exodus foraging strategies, and nesting site location. A causal relationship is further evidenced by the lack of a statistically significant difference in the density of bathymetric breaks between the two datasets when they are not analyzed by zone. This indicates that nesting location improves both male *and* female foraging strategies, and this link helps to explain the distribution of Audubon's Shearwater breeding locations in the Caribbean.

Understanding the specific conditions preferred by males and females, as shown by this paper, could have important consequences for future conservation efforts. Conducting surveys for Audubon's Shearwater is difficult, owing to their nocturnal nesting behavior (Trimm 2004). The sheer number of islands in the Caribbean where the birds could nest further compounds the problem. By looking for islands that lie at the extremes of the foraging area distributions preferred by both males and females, potential locations for shearwater nesting could be quickly identified and surveyed. With targeted information, shearwater colonies could be more easily located.

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