Climate change, heightened hurricane activity, and extinction risk for an endangered tropical seabird, the black-capped petrel *Pterodroma hasitata*

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ABSTRACT: The destructiveness of major (Category 3 to 5) hurricanes along the United States Atlantic Ocean seaboard has been recognized for centuries. While the effects of hurricanes on coastal ecosystems are well known, the influence of hurricanes on pelagic seabirds is difficult to assess. During the annual Atlantic hurricane season (~1 June to 30 November), the endangered black-capped petrel *Pterodroma hasitata* aggregates in Gulf Stream habitats from Florida to North Carolina. On at least 8 occasions over the past century, hurricanes have driven petrels far inland (sometimes as far as the Great Lakes), suggesting the demise of 10s to 100s of individuals. This paper models >100 yr of data to characterize and compare key aspects of hurricanes that did and did not drive petrels inland. Our model suggests that the predicted increase in the frequency of Category 3 to 5 hurricanes in the region due to climate change could nearly double the expected number of wrecked petrels over the next century and place an endangered species at greater risk of extinction.

KEY WORDS: Petrel · Hurricane · Gulf Stream · Climate change · Mortality · Wreck · North Atlantic

INTRODUCTION

On a decadal basis, the 20th century included quiet periods for major hurricanes (1970s, 1980s, and early 1990s) as well as periods of heightened activity (1940s, 1950s, early 1960s, mid-1990s through mid-2000s) (Landsea et al. 1999). Recently, global climate models suggest that rising ocean sea-surface temperatures may increase the frequency and intensity of hurricanes in the northwest Atlantic Ocean (Knutson & Tuleya 2004, Michaels et al. 2006). Models predict that over the next century, major hurricanes are expected to make landfall from Florida to North Carolina at nearly double their historical rates (Bender et al. 2010, Turner 2011), with some observations suggesting that such a change has already occurred (Trenberth 2005, Mann et al. 2009).

For more than a century, ornithologists have noted seabirds displaced inland following major hurricanes (Saffir-Simpson Wind Scale Categories 3 to 5) that struck the eastern seaboard of the United States (e.g. Lindahl 1899, Allen 1904, Murphy 1936). Over the past 30 yr, with a notable increase in the number and strength of tropical cyclones in the North Atlantic (Emanuel 2005, Webster et al. 2005), 1000s of coastal and pelagic seabirds, comprising >40 species, have been killed or observed far inland by such storms (e.g. Fussell & Allen-Grimes 1980, Brinkley et al. 1997). Over the past 110 yr, dozens of displaced and dead black-capped petrels *Pterodroma hasitata* (BCPE), an endangered species (IUCN 2010), including 27 specimens found in the United States and 21 in southern Canada (Kaufman 1990, Curry 1996, Brinkley et al. 1997) have been documented (Table 1).

Table 1. *Pterodroma hasitata*. Major hurricanes making landfall north of Florida (1893 to 2003) with total count of black-capped petrel carcasses. (Dead or moribund petrels corroborated by photograph, specimen, or description. Does not include live petrels seen inland that may have died later.) Cape Verde refers to origination east of 36° W. Strength of hurricanes uses the Saffir-Simpson wind scale. Recurved refers to the hurricane's distance from the coast upon turning north in units of hurricane-force winds (62.5 nautical miles) — higher positive numbers indicate farther offshore

Year	Hurricane name	Cape Verde	Origin (long., °W)	Landfall month	Landfall lat. (°N)	Max. strength	Landfall strength	Landfall angle (°)	Recurved (radii)	Carcasses
1893	Sea Islands (No. 6)	Yes	20	Aug	32	3	3	45	−1	5
1898	No. 7	No	58	Oct	30	4	3	90	−7	3
1933	Chesapeake Potomac	No	48	Aug	36	3	2	135	−2	1
1938	New England	Yes	22	Sep	41	5	3	90	9	1
1955	Connie	Yes	36	Aug	35	4	2	180	0	1
1989	Hugo	Yes	20	Sep	33	5	4	90	−6	9
1996	Fran	Yes	21	Sep	34	3	3	90	−7	26
2003	Isabel	Yes	31	Sep	35	5	2	90	−9	2
										Total = 48

With an estimated breeding population of 1000 to 2000 pairs (Lee 1999, Brooke 2004), the susceptibility of BCPE to major hurricanes is of concern.

Here, we tested the hypothesis that the effects of climate change—operating through the frequency and intensity of Atlantic tropical cyclones—could further threaten this species. To test this hypothesis, we examined 110 yr of hurricane data and modeled the attributes of hurricanes that caused—and did not cause—observed mortality of BCPE. Through this modeling, we: (1) described the critical characteristics of hurricanes that threaten BCPE and (2) quantified the potential consequences of climate change and heightened hurricane activity on the population of this species over the coming century.

MATERIALS AND METHODS

We conducted an exhaustive search of museum collections and literature for storm-wrecked specimens of black-capped petrel *Pterodroma hasitata*. Because the species is strictly pelagic, it was relatively easy to link specimens to particular tropical cyclones. Where feasible, we attempted to determine the age of wrecked birds, in order to consider effects of mortality on population dynamics.

Specimen and tropical cyclone data

The disposition of BCPE carcasses salvaged between 1893 and 2003 was largely derived from: the ORNIS data portal (http://ornisnet.org; accessed on August 31, 2011) and the Canadian Biodiversity Information Facility, which are national catalogs of ornithological holdings in museums. We also re-

viewed seasonal sightings summarized in the regional reports of 'North American Birds' and predecessor journals. We then made direct communication with collection managers and/or curators from the following museums where specimens of the species were known (or suspected) to reside: American Museum of Natural History, New York, NY; Birdcraft Museum, Fairfield, CT; Buffalo Museum of Science, Buffalo, NY; Canadian Museum of Nature, Gatineau, QC; Carnegie Museum of Natural History, Pittsburgh, PA; Cornell University–Museum of Vertebrates, Ithaca, NY; Museum of Comparative Zoology, Harvard University, Cambridge, MA; North Carolina Museum of Natural Sciences, Raleigh, NC; Peabody Museum of Natural History, Yale University, New Haven, CT; Royal Ontario Museum, Toronto, ON; Smithsonian National Museum of Natural History, Washington, DC; and University of Connecticut Biological Research Collections, Storrs, CT. For each specimen, we requested information on location, date of collection, sex, and age (via molt, skull ossification, and bursa development). We linked each specimen to a specific tropical cyclone based on collection date. All carcasses were found within 3 wk of the associated hurricane's passage (most within 1 to 10 d), with the last-salvaged tending to be the most decomposed. Displaced *live* petrels were seen in Lake Erie, Ontario, for 2 wk following Hurricane Fran (Brinkley et al. 1997), so relatively fresh carcasses could be found for weeks. To assess the ages of wrecked petrels, we evaluated patterns of molt and feather wear (per Imber 1984, Brown et al. 1986). In such cases, the primary criterion to distinguish hatch-year birds from adults (all ages after hatch year) is the uniformly fresh, unworn plumage of juveniles versus the patchwork of crisp and worn feathers characteristic of older birds.

Table 2. *Pterodroma hasitata*. Major hurricanes making landfall north of Florida (1893 to 2003) with no associated black-capped petrel carcasses. Cape Verde refers to origination east of 36° W. Strength of hurricanes uses the Saffir-Simpson wind scale. Recurved refers to the hurricane's distance from the coast upon turning north in units of hurricane-force winds (62.5 nautical miles) — higher positive numbers indicate farther offshore

Year	Hurricane name	Cape Verde	Origin (long., °W)	Landfall month	Landfall lat. (°N)	Max. strength	Landfall strength	Landfall angle (°)	Recurved (radii)
1893	No. 4	Yes	36°	Aug	41	3	1	135	4
1893	No. 9	Yes	25°	Oct	33	3	3	0	1
1896	No. 2	No	59°	Sep	42	3	1	90	10
1899	San Ciriaco	Yes	31°	Aug	35	4	4	60	4
1916	No. 2	No	52°	Jul	33	3	1	180	7
1916	No. 4	No	71	Jul	33	3	2	90	−3
1933	No. 13	No	58°	Sep	35	3	2	180	0
1944	Great Atlantic	No	58°	Sep	41	4	2	135	2
1954	Hazel	No	59°	Oct	34	4	4	135	0
1955	Diane	No	43°	Aug	34	3	1	90	−3
1955	Ione	No	43°	Sep	35	3	1	135	−3
1959	Gracie	No	68°	Oct	32	4	3	90	8
1961	Esther	Yes	32°	Sep	44	4	0	135	9
1969	Gerda	No	77°	Sep	45	3	2	135	18
1976	Belle	No	73°	Aug	41	3	1	90	11
1979	David	Yes	36°	Sep	31	5	1	135	−1
1984	Diana	No	77°	Sep	34	4	1	45	3
1985	Gloria	Yes	24°	Sep	41	4	1	180	4
1991	Bob	No	75°	Aug	41	3	2	180	5
1996	Bertha	Yes	34°	Jul	34	3	2	135	3
1998	Bonnie	No	48°	Aug	34	3	2	180	2
1999	Floyd	No	46°	Sep	34	4	2	135	3

Predicting wrecks based on storm characteristics

Because not all storms produced specimens of BCPEs (i.e. 'wrecks'), we compared characteristics of storms that resulted in wrecks with those that did not. Information on the path, strength, and timing of tropical cyclones was obtained through internet archives (www.nhc.noaa.gov/pastall.shtml). All attributes of hurricanes summarized in Tables 1 & 2 (hurricane name, maximum strength, etc.) were derived from NOAA data. Using model selection, we fitted data on the occurrence/non-occurrence of wrecks resulting from major storms (Category 3 or greater) off the eastern seaboard between 1893 and 2003. During this time, there were a total of 30 major landfalling hurricanes, of which 8 produced wrecks (Fig. 1, Table 1). Of these, 6 were 'Cape Verde' hurricanes that originated east of 36° W. Seven of the 8 storms struck the coast directly (only 1 collided with the coastline at an angle of <45° or >135°), and all made landfall as Category 2 storms or greater. Hurricanes that had nearly parallel paths to the coastline (i.e. landfall angles that were very acute or obtuse) seldom produced mortality or inland petrels (Table 2). From these observations, we generated a candidate set of models with storm-specific occurrence/non-occurrence of wrecks as a binomial response (logit link) and, fixed effects of Cape Verde classification (categorical), month (continuous), landfall strength (categorical), recurvature (categorical), latitude at landfall (continuous), landfall angle (continuous), maximum storm strength (categorical), and radii at recurve (continuous). Maximum hurricane-force winds generally extend 62.5 nautical miles (n miles; ~115.75 km) from the center of a storm (also termed the 'strike circle'); therefore, to quantify how far from the coast a hurricane turned north (recurved), we used the number of hurricane-force wind radii as the unit of measure — with higher positive numbers indicating farther offshore and lower negative numbers signifying turns occurring farther inland. Using StepAIC (a library for the R statistical package) we identified a set of 4 model formulations that resulted in the greatest parsimony, and then calculated the model weights of these models based on their Akaike's information criterion (AIC) scores (Table 3).

Simulating future wrecks

In order to simulate the expected number of petrel mortalities due to storms over the next 100 yr, we: (1) generated 100 000 random draws of integers from a Poisson distribution fitted to data on the number of yearly storm occurrences between 1893 and 2003,
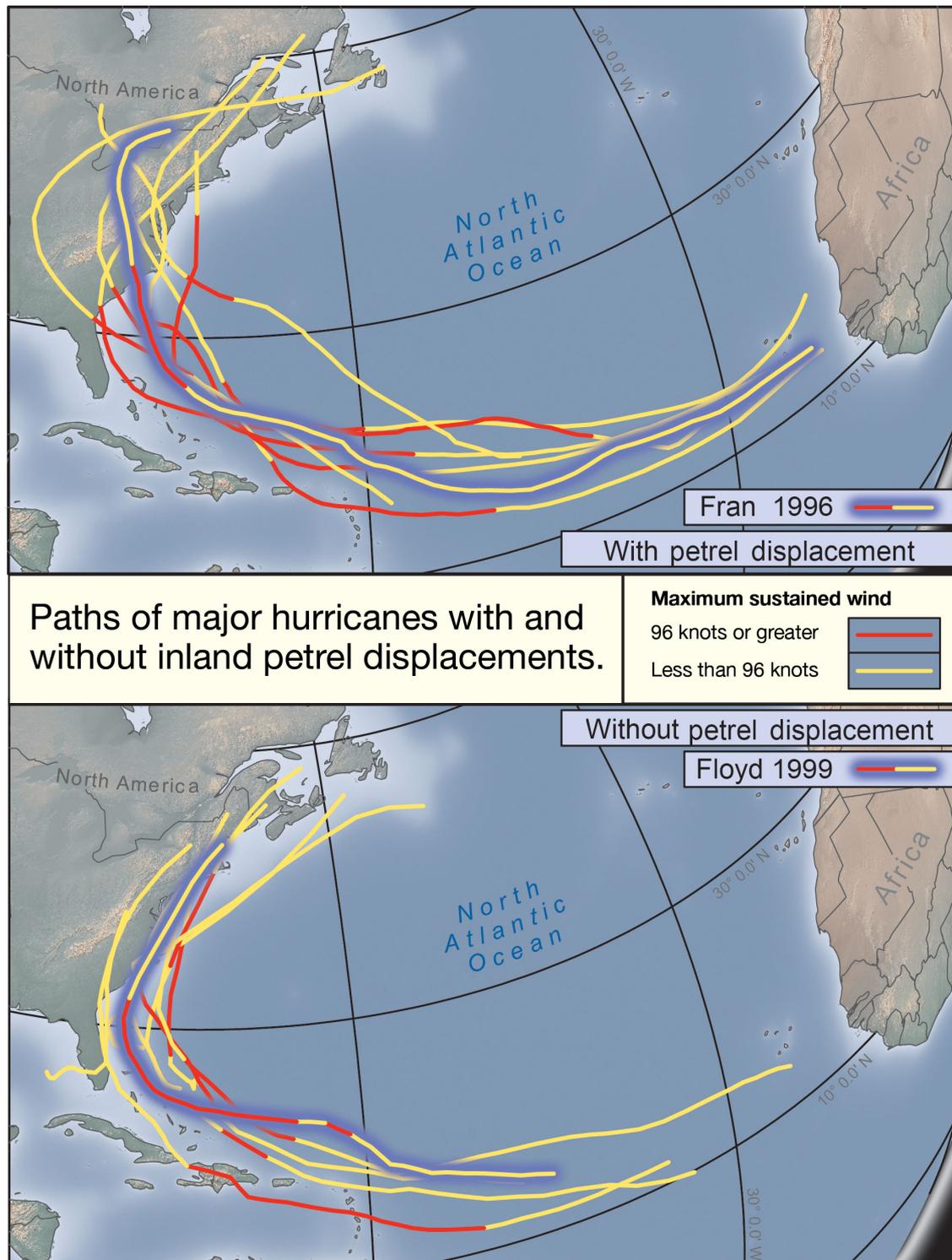
Fig. 1. *Pterodroma hasitata*. Top: paths of all major landfalling hurricanes (1893 to 2003) that displaced black-capped petrels inland exhibit origins near Cape Verde and strike the coast before recurving. Highlighted path is that of Hurricane Fran (1996), a typical storm-track for this category. Bottom: paths of all major landfalling hurricanes (1960 to 2003 only) that did not displace black-capped petrels show more westward origins and recurving trajectories than those producing petrel specimens. Highlighted path is that of Hurricane Floyd (1999), a typical storm-track for this category. Key characteristics (e.g. maximum strength, landfall date, etc.) for each hurricane are summarized in Tables 1 & 2. Map generated using NOAA Coastal Services Center data (http://csc-s-maps-q.csc.noaa.gov/hurricanes/viewer.html)

Table 3. *Pterodroma hasitata.* Goodness-of-fit models and scores of Akaike's information criterion (AIC). Variables include: whether a Cape Verde-type hurricane (VERDE), latitude at landfall (LANDFALL_LAT), strength at landfall (LAND_STRENGTH), distance from coast when hurricane turned north (RECURVE_RAD), maximum hurricane strength (MAX_STRENGTH), angle of hurricane landfall along coast (ANGLE), and month of landfall (MONTH)

Model formulation	AICc	ΔAICc	Weight
VERDE + LANDFALL_LAT + LAND_STRENGTH + RECURVE_RAD	25.03	0	0.49
VERDE + LANDFALL_LAT + MAX_STRENGTH + LAND_STRENGTH + RECURVE_RAD	25.93	0.9	0.31
VERDE + MONTH + LANDFALL_LAT + MAX_STRENGTH + LAND_STRENGTH + RECURVE_RAD	27.46	2.43	0.14
VERDE + MONTH + LANDFALL_LAT + MAX_STRENGTH + LAND_STRENGTH + ANGLE + RECURVE_RAD	29.825	4.22	0.06

(2) re-sampled the coefficient values for the models in Table 3 with replacement using storm data between 1893 and 2003, and (3) generated random draws from a log-normal distribution fitted to data on the number of BCPEs present off the eastern seaboard based on monthly boat-based transects between July and September (month included as a continuous effect). For 100 000 simulations, annual mortality in each of the next 100 yr based on simulated storm occurrences for each year (based on random draws in 1 above), their likelihood of causing wrecks (based on the coefficient draws in 2 above), and the number of birds wrecked (based on random draws in 3 above) was derived. The likelihood that storms caused wrecks was calculated based on model averaging (Table 3). In other words, we used predictions from each model in proportion to their model weights. To evaluate the overall model fit within the candidate model set used, we conducted a receiver-operating characteristic (ROC) analysis to assess the sensitivity and specificity of the model with the lowest AIC score (Fig. 2). The area-under-the-curve score (true positive rate) of 0.943 resulting from this analysis suggests that our candidate model set was well specified.

Predicting hurricanes from climate change

Recent stochastic and dynamic climate models predict a slight increase in the intensity of future North Atlantic hurricanes (7 and 10.3%, Turner 2011 and Emanuel et al. 2008, respectively), largely due to the increased genesis of long-lived and powerful Cape Verde hurricanes (Knutson et al. 2010). Bender et al. (2010) anticipate that landfall rates for Category 4 to 5 hurricanes will increase 10% per decade over the next century—doubling their incidence by 2100. Similarly, Turner (2011) forecasts that Category 3 to 5 hurricanes will nearly double in landfall frequency

between 2011 and 2015 and that continued 'warm scenario' conditions will promote increased genesis of Cape Verde hurricanes. Consequently, we integrated a 1%-per-year increase in the incidence of major hurricanes over the next 100 yr to our model.

RESULTS

Wrecked petrels

In the literature and museum records, we located at least 82 inland records of black-capped petrels *Pterodroma hasitata* (1893 to 2003) associated with the passage of tropical cyclones that were classified as 'major' (Saffir-Simpson Categories 3 to 5) during some point in their development. No petrel carcasses were recovered after a major (or minor) hurricane made landfall in Florida, so we restricted our analysis to hurricanes that came ashore north of Florida (Tables 1 & 2). Petrels have occasionally been seen
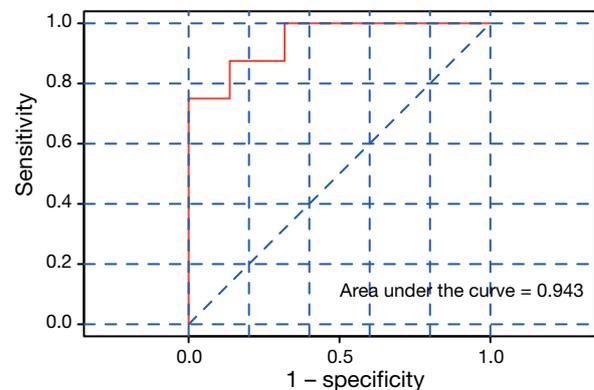

Fig. 2. Plot of the relationship between true positive (sensitivity; *y*-axis) and false positive rate (1 – specificity; *x*-axis) based on the parameters derived from the model with the lowest score of Akaike's information criterion (AIC) identified in Table 3. The area under the curve term indicates the true positive rate resulting from the model prediction

from shore during smaller (Categories 1 to 2 maximum) hurricanes. So far, however, none of the smaller magnitude storms have displaced petrels inland or resulted in mortality (based on museum holdings). For instance, although 3 petrels were seen from shore in North Carolina following the landfall of Category 1 Hurricane Ophelia in 2005, no dead petrels were reported (Dinsmore & Farnsworth 2006). Since minor hurricanes and tropical storms do not appear to be significant mortality agents, we have excluded such records from our analysis. Of the 82 sight records of inland BCPEs, 48 were substantiated by a bird-in-the-hand. The present study concentrated only on the most recent carcass material, from 1989–2003, or 37 total specimens, because birds salvaged in recent decades tended to have more consistent data recorded for molt, sex, and body condition.

The Carnegie Museum of Natural History prepared 2 skins of BCPEs associated with Hurricane Hugo (1989) and another after Hurricane Fran (1996); all 3 showed evidence of molt in rectrices or contour feathers, strongly suggesting they were adult birds. Birds only a few months past fledging would almost certainly not be in active molt of rectrices (Imber 1976, Warham 1996). Also associated with Hurricane Fran, 8 petrels stored at the Royal Ontario Museum (ROM) showed evidence of molt and were categorized as adults. Only 4 of those 8 individuals were salvaged in good enough condition to allow evaluation of the bursa of Fabricius. None had a bursa, confirming their status as likely breeding-age adults (Broughton 1994). Furthermore, of the 8 intact skulls among the ROM specimens, all showed full ossification (i.e. fusion) of the frontal/prefrontal bones, confirming their ages as after hatch-year (Harper 1978). Two Smithsonian specimens wrecked by Hugo were molting females, but 1 of them had a bursa, indicating that it was greater than 1 yr old but likely of pre-breeding age. At the Cornell University Museum of Vertebrates, the 2 petrels salvaged after Fran have uniformly fresh plumage, and were categorized as hatch-year birds. Thus, in our sample of 15 specimens, adult birds outnumbered young (probable yearlings) birds by a ratio of 13:2. This adult bias is not surprising given that the ratio of adult to hatch-year birds collected at sea off North Carolina is 56:3 (T. R. Simons et al. unpubl. data). While males outnumber females by a ratio of 2:1 in those specimens (not 9:1 as reported by Lee 1999), we found that among the 13 wrecked petrels for which sex could be determined, an opposite sex ratio was apparent (5 males:8 females). Although our model is based on deaths of individuals, it assumes a 50:50 sex ratio.

Mechanism of displacement

A direct path toward the coast is key to whether a hurricane wrecks petrels or not (Tables 1 & 2). We hypothesize that when west-approaching hurricanes recurve (turn north to northeast) north of Florida, the flight space and prevailing winds that exist between the storm's perimeter and the coastline serve as a corridor through which birds are funneled to shallower, nearshore waters along the eastern seaboard (Fig. 3). Indeed, on average, hurricanes that did not produce specimens tended to recurve when almost 240 n miles east of the coast, while those producing carcasses pushed inland nearly 180 n miles before turning north (Tables 1 & 2).

Simulated consequences for breeding population

The mode value in our simulation (Fig. 4) suggests that over the next century, in the absence of climate change, landfalling hurricanes would most likely kill approximately 437 petrels. Because of the preponderance of adults among the wrecked specimens (>80%) and in the population at sea off the southeastern United States (95%), this represents an anticipated loss of at least 415 breeders—or 10.4% of the 4000 individuals estimated in the current breeding population. About 7% of the simulations result in
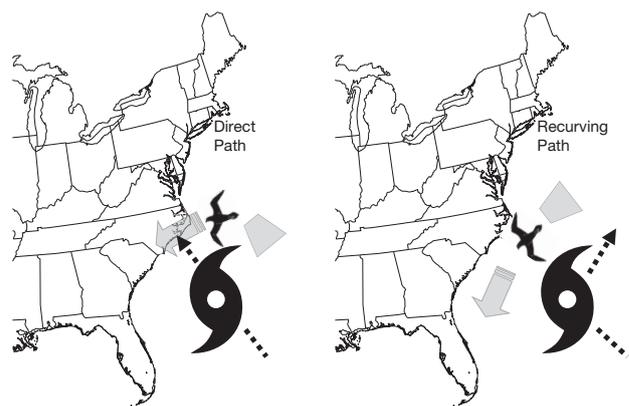
Fig. 3. *Pterodroma hasitata*. Mechanism of black-capped petrel inland displacement or non-displacement by hurricanes. On average, landfalling major hurricanes that did not produce specimens turned north (recurved) when >240 nautical miles offshore, while petrel-producing hurricanes turned north after pushing 180 nautical miles inland. When North Atlantic hurricanes recurve, the extra over-water flight space that is created between the storm's perimeter and the coastline serves as a corridor through which petrels are funneled to shallower, nearshore waters. When hurricanes make landfall on a direct course, no such corridor is created and petrels are swept inland
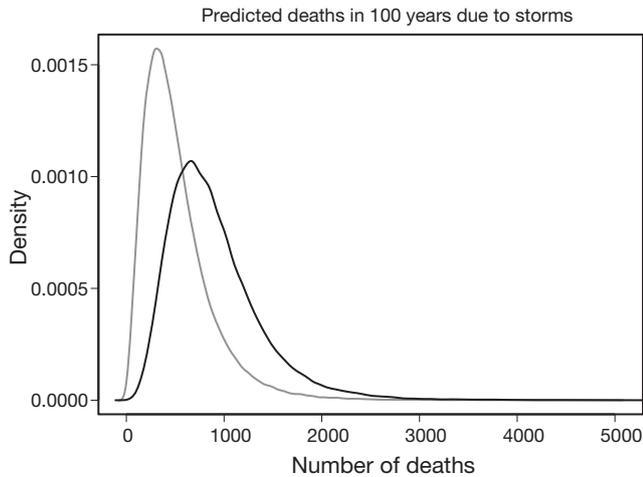
Fig. 4. *Pterodroma hasitata*. Predicted deaths of black-capped petrels in 100 yr due to storms. If the hurricane activity over the next century is similar to that over the last century, across 100 000 simulations, the median cumulative number of deaths of black-capped petrels is 437 (grey line). The chance that >1050 (or one-quarter of the estimated breeding population) will die is 7 %. If the rate of major landfalling hurricanes rises 1 % annually due to climate change (doubling over the next century as predicted), the median cumulative mortality is 807 petrels (black line), with a 3 % chance that 2100 individuals (half the breeding population) would die due to hurricanes

mortality of >1050 individuals (or 1000 breeders)— which would reduce the extant breeding population by 25 %. If the rate of major landfalling hurricanes increases by an annual rate of 1 % due to climate change (Bender et al. 2010, Turner 2011), doubling by the end of this century, the median cumulative mortality is 807 petrels, with a 3 % chance that 2100 individuals would die due to hurricanes. However, though some estimate the breeding population to be ~4000 individuals (Brooke 2004, Keith 2009), Lee argued more than a decade ago (Lee 1999, 2000) that the number of breeders was only 1200 to 2600 individuals — which would put the entire breeding population at risk of extinction if the cumulative mortality exceeds 1200 over the next century.

DISCUSSION

Considerable direct mortality from hurricanes has occurred over the past century

Over the last 2 decades, the documented hurricane mortality of black-capped petrels *Pterodroma hasitata* has totaled >30 individuals, although many of the additional 50 individuals observed far inland were probably weakened birds that also perished. Considering the vast areas of ocean and land that these storms affect, along with the relative dearth of people who actively seek hurricane-displaced seabirds (and even smaller number engaged in specimen salvage), the total number of BCPEs killed by hurricanes is certainly far greater than that documented by museum specimens. By systematically surveying a subset of shorelines around Lake Erie and Lake Ontario, Curry (1996) conservatively estimated that for every specimen salvaged or seen dead/floating but unretrieved (n = 23), an additional 2 petrels were killed but not found, bringing the total regional mortality to about 70 birds. At least 7 BCPEs were recovered after Hurricane Hugo, and Kaufman (1990) asserted that many times that number must have been killed by the storm. After both hurricanes Hugo and Fran, petrels not only wrecked on large bodies of water, but also in high, remote terrestrial sites—like mountaintops— that could not be systematically surveyed (Brinkley et al. 1997).

The loss of 10s to 100s of individuals during a *single* hurricane might not represent a demographic threat to a species with a world population estimated at 2000 breeding pairs (Brooke 2004). However, many climate change models suggest that rising sea-surface temperatures in the tropical North Atlantic will lead to future hurricanes that are more intense and/or greater in number (Knutson & Tuleya 2004, Michaels et al. 2006). Petrels, having evolved in a system of cyclonic activity that is subject to such multi-decadal variability, should perhaps be resilient to normal extremes. However, we propose that their populations, facing numerous other conservation challenges (nest site destruction, introduced predators, direct harvest by humans, etc.) will become increasingly vulnerable to additional decline if the coming decades/centuries continue to show cyclonic activity in the North Atlantic Ocean that is markedly higher than the long-term average (Trenberth 2005).

Petrels frequently aggregate in the likely paths of hurricanes

During 67 offshore surveys in July to September near Cape Hatteras, between 1992 and 1998, the lead author and Brian Patteson encountered extremely dense concentrations (>500 individuals seen per day) of BCPEs at sea twice (3 % of daily counts) and moderately dense concentrations (>150 individuals) 10 times (15 % of daily counts). The species' propensity for aggregation near Cape Hatteras, North Carolina

(the area of most frequent hurricane landfall in the eastern United States) during the height of the Atlantic tropical storm season is particularly alarming, because moderately and extremely dense aggregations of petrels would be expected to be in the *direct path* of about 1 in 6 and 1 in 33 major hurricanes approaching Cape Hatteras, respectively. Haney (1987) documented similarly elevated abundances off South Carolina and Georgia, so the chance intersection between a moving hurricane and an aggregation of petrels is not confined to Gulf Stream waters off North Carolina.

Petrel flight tendencies promote vulnerability to displacement

In the Northern Hemisphere, seabirds to the north of a cyclone would tend to take a westward course when the prevailing winds shift from an easterly to a more northern component (Blomqvist & Peterz 1984), a behavior that would promote escape from recurving hurricanes. Note that the median size of petrel-producing hurricanes at landfall was Category 3 compared to Category 2 for those without carcasses; the smaller hurricanes would be surrounded by smaller wind fields (narrower radii of hurricane-force winds), broadening the crosswind/tailwind corridor for birds described above. Indeed, Adams & Flora (2010) recently demonstrated that *Pterodroma* petrels tend to travel with quartering tailwinds, allowing them to circumnavigate mega-scale high-pressure systems. Such a tendency would tend to disperse birds flying to the south of a hurricane away from the system; while petrels located north and west of the system would be vulnerable to being pushed onshore by large hurricanes making direct landfall. Whereas more than one-quarter of major hurricanes that made landfall north of Florida produced inland petrels, none of the 11 major hurricanes that struck Florida between 1893 and 2003 produced a single petrel specimen. We believe that Florida's narrow, peninsular shape and proximity to the Gulf of Mexico probably provides an opportunity for petrels to escape to the southwest.

Numerous hurricanes have blown BCPEs outside their 'normal' marine range—to colder, continental shelf waters as the storms have progressed northward in latitude (Mörzer Bruyns 1967, Finch 1972, Dinsmore & Farnsworth 2006). Such observations of multiple petrels along the advancing margins of hurricanes are contrary to the proposition that petrels are likely entrained in the calm eyewall of hurricanes

and disperse after landfall (Murphy 1936). Sooty terns *Onychoprion fuscatus* are also strictly pelagic and appear particularly vulnerable to hurricane-driven displacements (Murphy 1936, Brinkley 1999). Murphy's (1936) description of flocks of sooty terns *preceding* the arrival of hurricanes in the Lesser Antilles is consistent with the mechanism of displacement for that species and BCPEs witnessed along the east coast of the United States. As the Gulf Stream between Florida and North Carolina appears to represent the principle foraging range for adult BCPEs (Haney 1987), any factor that displaces petrels far from the center of their known range is likely detrimental.

During the Atlantic hurricane season, satellite-tracking studies have revealed that the Bermuda petrel *Pterodroma cahow*, another critically endangered petrel, tends to forage in 2 principal areas—near the Azores, and north and west of Bermuda (Madeiros 2010). Both areas lie within the influence of Cape Verde hurricanes, and, furthermore, these foraging hotspots (used by the species in the non-breeding season) are located north and west of such advancing hurricanes. Because Bermuda petrels are known to use tailwinds to 'slingshot' around the perimeter of storm systems (Madeiros 2010), the positioning of these key foraging areas is likely to raise the species' vulnerability to being pushed inland as individuals transit downwind.

Persistence of Gulf Stream path during climate change should sustain petrels

At sea, the BCPE appears to be an obligate of Gulf Stream waters off the southeastern United States and aggregates where deepwater upwelling occurs (Haney 1987, Hass 1997). Hence, any changes in the circulation of the Gulf Stream due to climate change might affect the species. Lynch-Stieglitz et al. (1999) demonstrated that during the last glacial maximum, the strength of Gulf Stream transport was only two-thirds of that seen today. While it is difficult to predict how reduced transport in the Gulf Stream might affect the frequency and magnitude of many dynamic sources of upwelling (e.g. meanders and eddies), static upwelling sites, where upwelling is topographically induced (like the Charleston Bump and Cape Hatteras slope) seem likely to persist over time. Several authors have shown that a shutdown of the 'global conveyor belt' is possible during either cold or warm conditions (Alley et al. 1997, Broecker 1997). Although the Gulf Stream is likely to weaken during

such a thermohaline collapse, its position is merely expected to switch from its present meridional course (heading northeast from Cape Hatteras), to a zonal heading (east from Cape Hatteras) (Matsumoto & Lynch-Stieglitz 2003, Rossby & Nilsson 2003). This should preserve the Gulf Stream's path (and processes) in the South Atlantic Bight, in the center of the petrels' pelagic range.

Climate change, human settlement and historic declines of tropical Atlantic petrels

Olson (1975) previously implicated Pleistocene 'environmental change' and associated shifts in marine productivity as leading to the decline and extinction of *Pterodroma rupinarum* and 2 other tropical tubenoses on St. Helena Island in the tropical South Atlantic. *P. rupinarum* bred on St. Helena at a comparable latitude (17° S) to BCPEs, and the already extinct Jamaica petrel *P. caribbaea* bred in the Caribbean (18° to 20° N), but declined markedly during non-glacial times. The final demise of both *P. rupinarum* and *P. caribbaea* coincided with human habitation. Recent conservation efforts for the critically endangered Bermuda petrel *P. cahow* have attempted to shift burrows/colonies to higher ground to minimize vulnerability to sea-level rise, hurricanes, and associated storm surges (Wingate & Talbot 2003). As their breeding population has grown and offshore surveys have become more frequent, Bermuda petrels have been found regularly in the Gulf Stream off North Carolina (Wingate et al. 1998, Patteson & Brinkley 2004) during the hurricane season, so it seems likely that someday this species too may appear inland among the wrecked. Because BCPEs breed on remote cliff faces in Hispaniola outside the hurricane season, they are not likely to suffer direct mortality at the nesting grounds—though hurricane-induced mudslides and destruction of vegetation could destroy burrows (Goetz et al. 2011).

Simulated hurricane-related mortality has population-level effects on petrels

When population viability analyses are used to estimate extinction risk for the long term, they usually account for episodic, but extreme catastrophes (e.g. 100 and 500 yr droughts, floods, etc.) that may lead to population bottlenecks or other adverse demographic effects. If the past century of hurricane data and seabird die-offs is representative of the long term, BCPEs will face a demographic threat from major Atlantic hurricanes for millennia. Much like migratory shorebirds that briefly aggregate at stopover sites, petrels frequently exhibit extreme aggregations in space and time. Thus, on the rare occasion that a petrel aggregation (or a known migratory or foraging hotspot) is in the path of a hurricane (or oil spill, etc.), elevated mortality will likely result.

Data from pelagic surveys suggest that moderate to extreme aggregations of BCPEs occur every 5 d at sea. Such propensity for aggregation (or flocking) means that a significant fraction of the world's population may be in jeopardy if they have happened to amass in the path of a hurricane that is: Category 3 or greater, on a direct course to make landfall, and arose in the eastern North Atlantic (Table 3). Using the past 110 yr as a baseline, our model suggests that, in the absence of climate change, the most probable scenario is the loss of about 10% of the estimated breeding population over the next century due to hurricane wrecks. When factoring in climate change—a gradual doubling in the frequency of major landfalling hurricanes—the likeliest mortality is about one-fifth of 4000 breeders. However, 1 in 33 simulations demonstrated a loss of 2000 breeders. Considering that 40% declines were already witnessed during a 2-decade lull in hurricane activity (Woods & Ottenwalder 1986), any projections of additional double-digit reductions are distressing. While the above percentages reflect the relative impacts if the breeding population is 2000 pairs (Brooke 2004, Keith 2009), Lee (1999, 2000) asserts that the number of breeders may be as low as 600 to 1300 pairs—which would magnify the proportional effects and produce a small chance that hurricanes might wipe out the entire the breeding population by 2111. Given that the species is already in rapid decline due to other sources of mortality and shows no signs of above-replacement population growth, the deaths of 2100 individuals (mostly breeders)—solely due to hurricanes—over the next century could either cause or significantly contribute to the species' demise. Since our mortality projections only examine the demographic threat posed by hurricanes, we strongly advocate for a greater understanding and mitigation of other mortality sources if the species is to avoid the risk of a population bottleneck, or worse, extinction.

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