Inter-Colony Differences in Wading Bird Flight Patterns in New York Harbor

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Introduction:

During the late 1970s and early 1980s herons and egrets began using New York Harbor's islands for breeding. With these islands transformed into active breeding colonies, the birds became the focus of many research initiatives. One such initiative is NYC Audubon's Harbor Herons Shore Monitoring Program which focuses on identifying wading bird foraging areas. During the breeding season of 2004, data relating to wading birds' flight activity was collected for two large, active colonies – Brother Islands colony and Hoffman colony.

Comparing the data collected from each colony pointed to inter-colony differences regarding the patterns of wading bird flight activity. These differences were surprising given the fact that both colonies were located in the same estuary and fairly similar across different criteria such as species composition, population size, and colony area size. This paper presents the differences observed during the Shore Monitoring Program of 2004 and offers possible reasons for their existence.

Methods:

The second year of the Harbor Herons Shore Monitoring Program researchers collected data on wading bird flight activity over a period of 11 weeks, from 4 June-15 August 2004 for two colonies in New York Harbor: Brother Islands colony and Hoffman colony (Fig. 1). Data was collected for the following bird species: Great Egrets (*Casmerodius albus*), Black-crowned Night-Herons (*Nycticorax nycticorax*), Snowy Egrets (*Egretta thula*) and Glossy Ibis (*Plegadis falcinellus*).

The island-colonies were monitored from shore locations close to the islands. Monitoring sessions consisted of morning and evening sessions, a methodology used in other wading bird studies (Erwin *et al.* 1991).[1] Sessions were conducted each week with each week alternating between morning and evening sessions, beginning with morning sessions. Morning sessions were held from 7-9:30 am and evening sessions were held from 5:30-

[1] The fact that not all compass directions were visible from these observation points wasn't considered a major difficulty since our observation points were probably located on the side of the colonies where most of the flight activity took place.

8:00 pm. Every colony was monitored at least one time each week[2] (Table 1). Binoculars and spotting scopes were used to identify different bird species.

The following information was recorded for birds observed leaving or entering the colonies: time of day, whether the bird was leaving or entering the colony, flight direction (one of eight major octants from the center of the colony), and species. The following abiotic conditions were noted during the session and updated hourly: air temperature in the shade, wind direction (one of eight major octants), cloud coverage over the colony, and whether it rained or not. Tide information was added later using NOAA tide tables; wind speeds at each colony were added from the website "weather.com." Monitoring was conducted by a group of volunteers, with Yigal Gelb supervising the data collection process throughout every session.

Figure 1. Map of the study area showing the wading bird colonies of Brother Islands and Hoffman.

Image courtesy of NY/NJ Baykeeper.

[2] During the last week, only one colony was monitored.

Table 1. Session Description, including Total Bird Count

Week No.	Date	Session Dropped	Colony	Start Time	Finish Time	Birds Counted
1	4-Jun	dropped	Hoffman	7:10	10:03	122
1	6-Jun	dropped	Hoffman	7:25	8:45	3
2	10-Jun		Brothers	17:10	19:40	180
2	11-Jun		Hoffman	17:45	19:45	171
2	12-Jun		Brothers	17:45	20:00	139
3	17-Jun		Brothers	7:00	9:00	207
3	19-Jun		Hoffman	7:20	9:15	144
4	25-Jun	dropped	Hoffman	17:35	19:00	96
4	26-Jun		Brothers	17:30	19:30	67
4	27-Jun		Hoffman	17:40	19:33	125
5	1-Jul		Brothers	7:00	9:00	160
5	2-Jul		Hoffman	7:30	9:10	120
5	3-Jul		Brothers	7:00	9:00	199
6	8-Jul		Brothers	17:40	19:40	81
6	10-Jul		Hoffman	17:10	19:15	150
7	15-Jul		Brothers	7:00	9:00	118
7	16-Jul		Hoffman	7:15	9:15	122
8	22-Jul	dropped	Brothers	17:40	19:40	64
8	23-Jul	dropped	Hoffman	17:45	19:45	62
8	24-Jul	dropped	Brothers	17:30	19:50	52
9	29-Jul	dropped	Brothers	6:00	8:00	49
9	30-Jul	dropped	Hoffman	7:15	9:15	21
9	31-Jul	dropped	Brothers	7:00	9:00	36
10	5-Aug	dropped	Brothers	17:30	1930	27
10	7-Aug	dropped	Brothers	17:30	19:30	20
10	8-Aug	dropped	Hoffman	17:30	19:30	3
11	15-Aug	dropped	Brothers	17:30	19:00	0

Study area:

Brother Islands:
This colony was situated on two islands in New York City's East River near the South Bronx (40° 47'-48'N, 73° 53'W) and included about 500 nesting pairs. The predominant species were black-crowned night-herons followed by great egrets and snowy egrets (Kerlinger 2004). There were no ibis on these islands. Most of the birds nested on the 7-acre island of South Brother with a smaller population of black-crowned night-herons nesting on the 20 acre island of North Brother. A large cormorant population was also nesting on South Brother Island. Monitoring took place from a deck located in Castle Oil (140th St. and Locust Ave.) which was WNW of the Islands. This location allowed for a good view of both Islands with North Brother Island 450 meters and South Brother Island

900 meters from the monitoring deck. Since monitoring took place from only this location, flight activity on the other side of the islands was obscured.

Hoffman Island:
This colony was situated on a dredge-spoil island off the east side of Staten Island in the Lower Bay area of New York Harbor (40° 34'N, 74° 3'W) and included about 500 nesting pairs. The predominant species were black-crowned night-herons followed by great egrets, snowy egrets and glossy ibis (Kerlinger 2004). All the birds nested on the 10 acre island of Hoffman with cormorants present as well. Most of the cormorants, however, nested on the nearby island of Swinburne. Monitoring took place from two locations: The main location was a gazebo on South Beach, corner of Father Capodanno Blvd. and Sand Ln., located NW of the Island. The second location was the gazebo at the end of the Pier of Seaview Av., located W of the Island. These locations allowed for a good view of both Islands and were about 1,300 meters from Hoffman Island. Since monitoring took place from only these locations, flight activity on the other side of the islands was obscured.

Analysis:

The data collected was analyzed on seven levels:

1. Morning/Evening Flight Averages: These represent average number of wading birds observed flying during morning and evening sessions at the colonies. The null hypothesis assumes that there are no significant differences between the colonies.

2. In/Out Flight Averages: These represent average number of birds observed flying in and out of colonies during morning and evening sessions at the colonies. For each colony, numbers are reported by species. The null hypothesis assumes that there are no significant differences between the colonies.

3. In/Out Flight Activity Levels: These represent the number of birds flying in and out of the colonies aggregated over 15 minute intervals. For each colony, only numbers of great egrets are reported for both morning and evening sessions. Since section 2 – In/Out Flight Averages – measured the relative differences in In/Out flight patterns, this section is more concerned with examining the differences between colonies as they relate to the level of activity over the sessions. The null hypothesis assumes that there are no significant differences between the colonies.

4. Flight Directions at the Colonies: These represent the percentage of birds observed flying in 8 major compass directions (N, NW, W, etc) at the colonies. Percentages are charted for all birds and by species. Compass directions are taken from the center of the colony. Numbers are aggregated across morning and evening sessions. For the concentric circle charts, all bars add up to 100% of the birds charted. Note that since the foraging areas are not necessarily located in the

same place relative to each colony, the null hypothesis does not assume that there are no significant differences between the colonies.

5. Flight Lines and Possible Foraging Areas: These represent wading bird flight lines to and from the colonies as well as possible foraging areas. Using the flight directions presented in section 4, as well as other data sources, an attempt was made to chart the wading birds' main flight lines and identify the foraging grounds of each colony. It is assumed here that flights in and out of the colonies were related to foraging (Maccarone and Brzorad 2000; Erwin et al. 1991). Lines in black rely on data from Harbor Herons Shore Monitoring Program from 2003 and 2004 seasons. Lines in red rely on other data, anecdotal information, or inference.

   For Brother Islands, data collected from the first year (2003) of the Harbor Herons Shore Monitoring by volunteers supervised by Andy Bernick of the college of Staten Island's Biology Dept. was useful in charting flight lines beyond the monitoring location of 2004. Data collected by Alison Siegel from Rutgers University's Graduate Program in Ecology and Evolution, anecdotal information from Kyle Spendiff, a wetlands specialist at NJ Meadowlands Commission, and surveys conducted by the Harbor Herons Shore Monitoring Program during 2004 were helpful in documenting the birds' foraging areas in NJ Meadowlands. For Hoffman, data collected by New York City's Dept. of Parks & Recreation's Natural Resources Group, anecdotal information from Andy Bernick of the College of Staten Island's Biology Dept. and surveys conducted by the Harbor Herons Shore Monitoring Program during 2004 were helpful in documenting the birds' foraging areas in and around Staten Island.

6. Species Composition: These represent the total and relative abundance of birds for the beginning and middle periods of the monitoring season based on the counts of birds flying in and out of the colony (i.e., not nesting counts). For each colony, numbers are reported by species and are calculated by aggregating one morning and one evening session from the beginning period (week 2 and 3) and one morning and one evening session from the middle period (week 6 and 7).

7. Regressions: The regressions test the hypothesis that outward-bound flight did not differ among colonies, weeks in the season, morning or evening sessions, bird species, cloudy or clear skies, various wind speeds and wind directions, air temperatures, tide levels and flooding or ebbing tides for tides at the colonies and at the suspected foraging grounds. These regressions are based on a linear probability model where the dependent variable is outward-bound flight from the colony. Raw counts were used for these regressions. Variables were recoded so that positive values signify the existence of the condition described in each variable's name; values of zero signify the inexistence of that condition as shown below:

Variables	Recoded Values
Flight out of colony (in_out)	1=flight out, 0=flight in
Brothers Isl. Colony (brother)	1=Brothers, 0=Hoffman
Week in the season (week)	2=second week, 3=third week, to 7
Evening session (obs_time)	1=evening session, 0=morning session
Great Egret (greg)	1=GREG, 0=other
Snowy Egret (sneg)	1=SNEG, 0=other
Black-crowned Night-Heron (bcnh)	1=BCNH, 0=other
Clouds over colony (cloud)	1=cloudy, 0=not cloudy
Wind speed (wind)	0=0 mph, 1=1 mph, to 22
Wind from NW, W, SW (wind_w)	1=wind from NW, W, SW, 0=other
Air temperature in shade (temp)	21=21 deg. C, 22=22 deg. C, to 35.
Tide height at colonies (td)	1=low, 2=medium, 3=high
Tide direction at colonies (td_dir)	1=flooding, 0=ebbing
Tide height at foraging area (td_f)	1=low, 2=medium, 3=high
Tide direction at foraging area (td_f_dir)	1=flooding, 0=ebbing

Week in season: Data from weeks 2-7 were use in these regressions, representing about a month (June 10 to July 16). This month was most likely the middle phase of the breeding season, since eggs and young chicks were apparent by week 2, and no fledged birds were seen until week 8.

Bird species: Glossy ibis were excluded from these regressions since they only nested on Hoffman but not on Brothers. The regressions were run with dummy variables for each of the three remaining species, and black-crowned night-herons were arbitrarily assigned a value of "0" in these regressions, which is why they are "dropped" in the regressions.

Wind: The variable for wind direction was recoded to include winds from north west, west, and south west. These directions were chosen since at both colonies most of the birds flew out in a west or southwest directions, making these winds appear as "headwinds" for birds flying out of the colony.

Tides: Regression 1 was run using tide information at the colonies. Since it is possible that tide patterns at the birds' foraging areas also influence their flight activity, and since tide cycles vary considerably across the Harbor, Regression 2

uses tide information at suspected foraging grounds instead of at the colonies. Information regarding tide height and direction was taken from NOAA tide tables available on the web at: http://coops.nos.noaa.gov/tides04/tpred2.html.
The 12 hour tide cycle was divided into flooding and ebbing phases, with tide level in each phase recorded as low, medium, or high over 2 hour blocks.
Tide information for Brother Islands colony was taken from measurements at North Brother. Tide information for Hoffman colony was taken from measurements at Fort Wadsworth. Tide information for Brother Islands' NJ Meadowland foraging grounds was taken from Fish Creek, Berrys Creek (in NJ Meadow lands) and for Hoffman's foraging grounds from Carteret (in the Arthur Kill).

In order to allow for a cross-colony comparison, data was truncated to ensure that all morning sessions and all evening sessions started and ended at the same time for both colonies. Intervals with complete overlap for all colonies ranged from 7:30-9:00 (1.5 h) for morning sessions (7 sessions in total), and from 17:45-19:30 (1.75 h) for evening sessions (7 sessions in total).

Morning/Evening averages, In/Out flight averages, In/Out flight activity levels, flight directions at the colonies, and regressions were calculated from data collected over weeks 2-7. As shown in Table 1, this includes four morning and four evening sessions at the colony of Brother Islands, and only three morning and three evening sessions at Hoffman. One session at Hoffman was dropped due to low visibility. The first week was dropped entirely because Brother Islands colony was not monitored. Weeks 8-11 were dropped entirely because flight activity dropped noticeably and newly fledged birds were being spotted, something which could have biased the data.

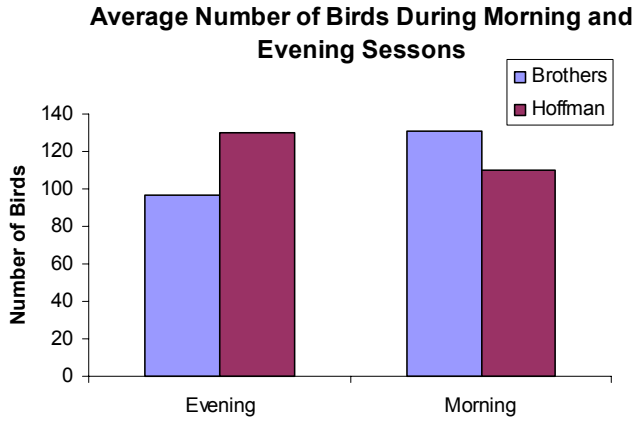
Results:

Over the course of 11 weeks 2,538 wading birds were counted leaving and entering the colonies of Brother Islands and Hoffman in New York Harbor. After the data was truncated to ensure that all sessions started and ended at the same time across colonies for both morning and evening sessions, the following numbers were recorded at each colony – 909 birds at Brothers over 8 sessions and 721 birds at Hoffman over six sessions.

1. Morning/Evening Flight Averages: **Average number of wading birds observed flying during morning and evening sessions at Brother Islands and Hoffman colonies.**

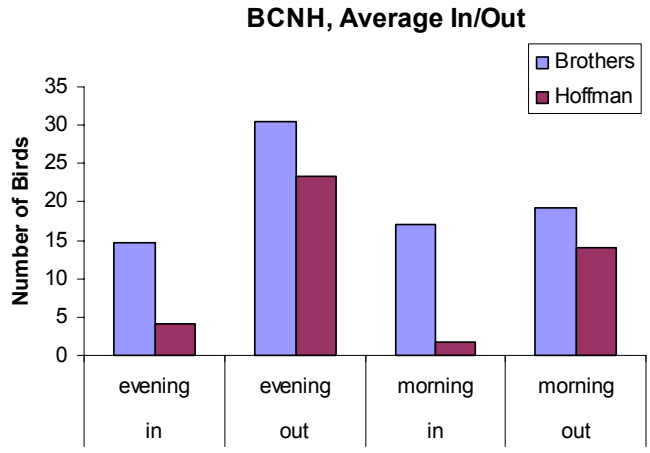
More birds were observed in the morning sessions compared to the evening sessions at Brothers Islands while the opposite was true for Hoffman with more birds observed in the

evening sessions compared to the morning sessions. Activity levels differ significantly between the two colonies (Fisher's exact test, P = 0.013).



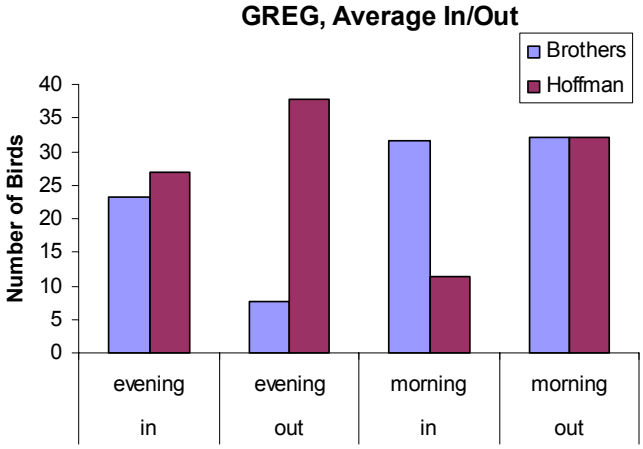
2. In/Out Flight Averages: **Average number of birds observed flying in and out of colonies during morning and evening sessions at Brother Islands and Hoffman colonies.**

During evening sessions at Brother Islands, more black-crowned night-herons were observed leaving the colony than entering it; the same was true for Hoffman colony. During morning sessions at Brother Islands, about equal numbers of birds were entering and leaving the colony, while at Hoffman more birds were leaving the colony than entering it. These numbers differ significantly between the two colonies (Chi 2 = 8.8, P = 0.031).

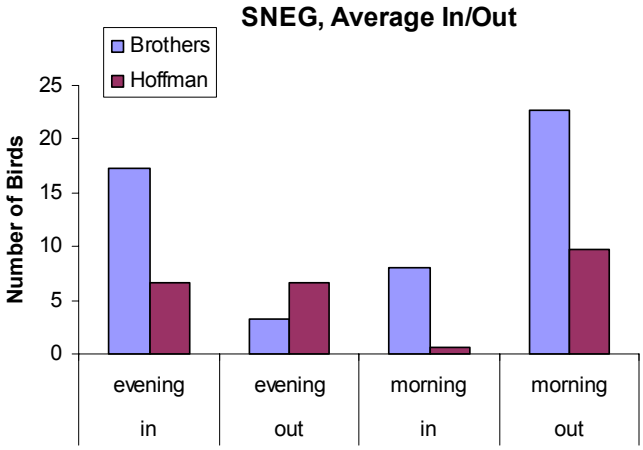


During evening sessions at Brother Islands, more great egrets were observed entering the colony than leaving it, while at Hoffman the *opposite* was true with more birds observed leaving the colony than entering it. During morning sessions at Brother Islands, about equal numbers of birds were entering and leaving the colony, while at Hoffman more

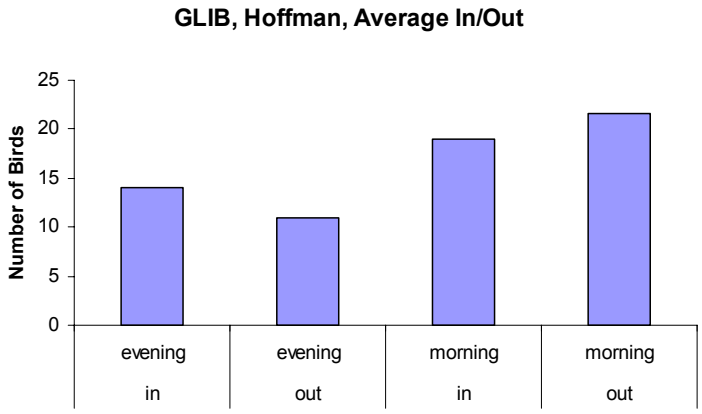
birds were leaving the colony than entering it. These numbers differ significantly between the two colonies (Chi 2 = 29.4, P < 0.001).



During evening sessions at Brother Islands, more snowy egrets were observed entering the colony than leaving it, while at Hoffman equal numbers of birds were observed leaving and entering the colony. During morning sessions at Brother Islands, more birds were observed leaving the colony than entering it; the same was true for Hoffman colony. These numbers differ significantly between the two colonies (Chi 2 = 8.4, P = 0.038).



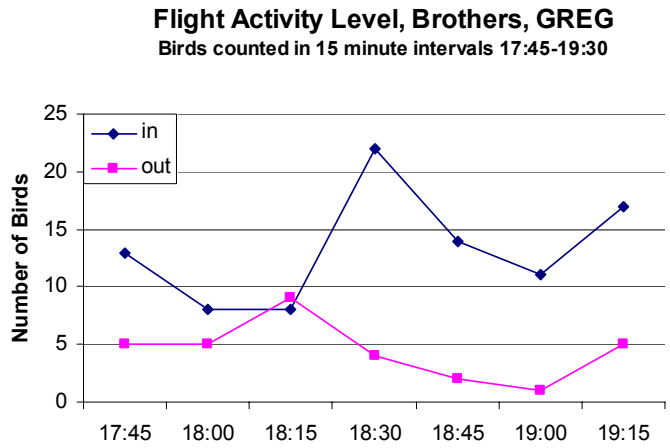
At Hoffman, about equal numbers of glossy ibis were observed leaving and entering the colony during morning and evening sessions. Higher numbers of ibis were observed during morning sessions.

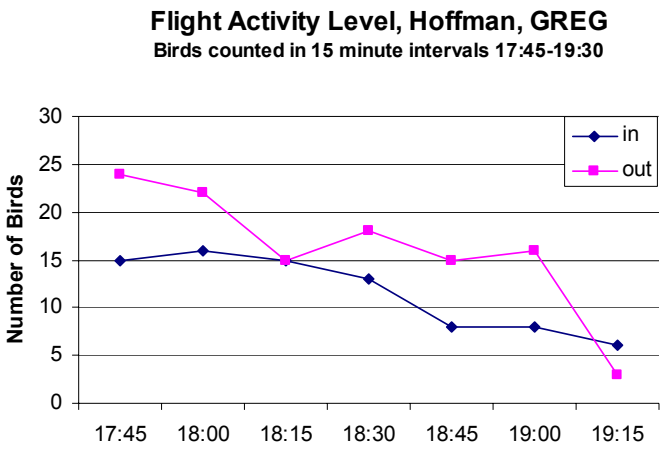


3. Flight Activity Level: **Total number of great egrets observed entering and leaving the colonies during 15 minute intervals, also referred to as "flight activity level," over both morning and evening sessions at Brother Islands and Hoffman colonies (Brothers includes 4 evening and 4 morning sessions; Hoffman includes 3 evening and 3 morning sessions).**

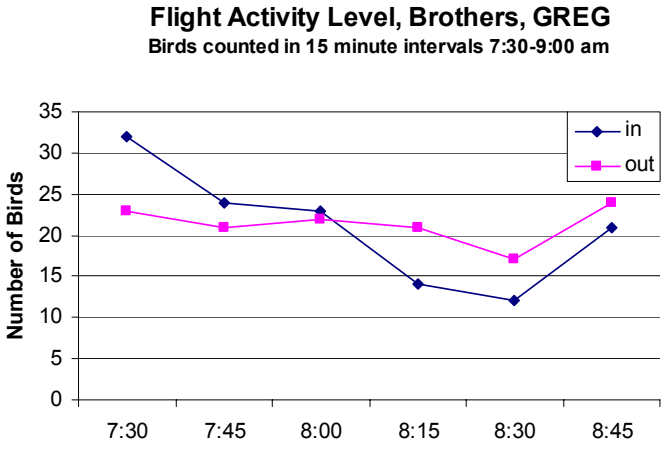
Only the flight activity level of great egrets is presented here for three main reasons: First, this bird species is easy to identify compared with snowy egrets, a fact which ensures higher accuracy. Second, the differences between colonies relating to In/Out flight activity were most pronounced for this species (highest Chi 2 value). Third, this species was present in large numbers at both colonies, allowing for a more meaningful comparison.

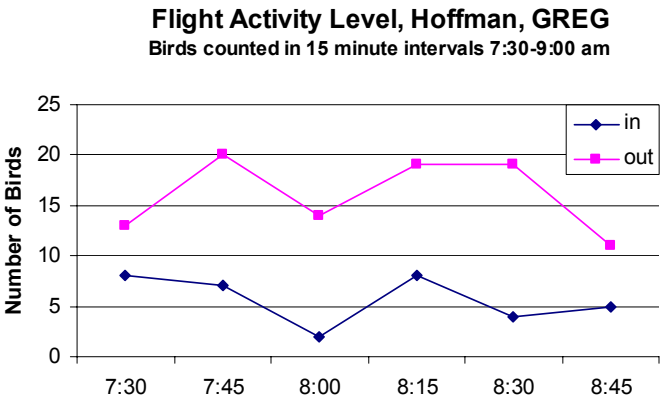
During evening sessions at Brother Islands, inward flight activity increased over the sessions, while outward flight activity remained fairly equal. At Hoffman, both inward and outward flight activity decreased over the sessions. (Chi 2 = , P =).





During morning sessions at Brother Islands, inward flight activity seemed to decrease over the sessions, while outward flight activity remained fairly equal. At Hoffman, inward flight activity remained fairly the same and outward flight activity seemed to peak during the sessions. (Chi 2 = , P =).

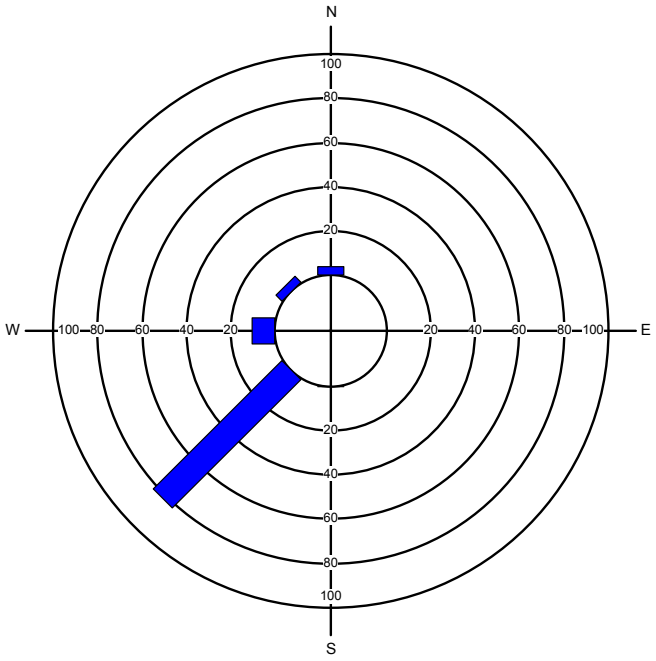




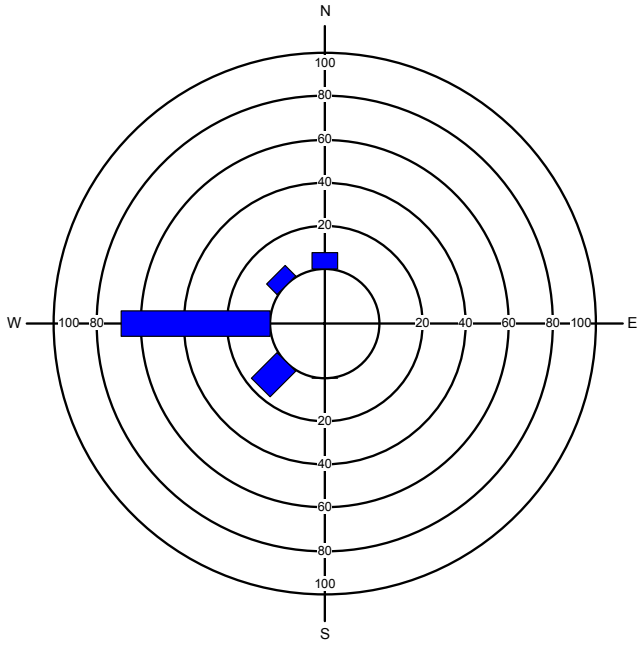
4. Flight Directions at the Colonies: **Percentage of birds observed flying in 8 major compass directions at Brother Islands and Hoffman colonies. Percentages are charted for all birds and for black-crowned night-herons and great egrets separately.**

At Brother Islands, 82% of all birds were observed flying south west. At Hoffman, 69% (including ibis) were observed flying west. Hoffman seems to have somewhat more dispersion in its flight lines. But when ibis are not included, Hoffman seems to have noticeably more dispersion compared with Brother Islands.

Brother Islands, Flight Directions for All Birds (all birds = 100%)

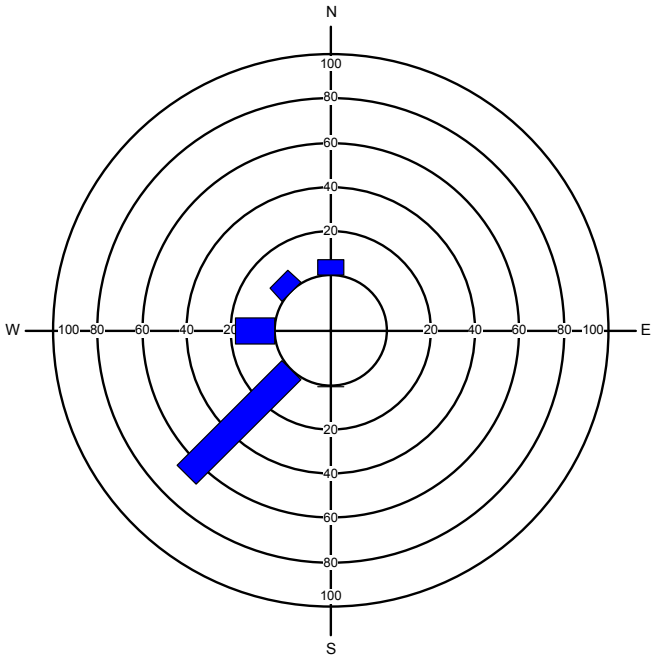


Hoffman Island, Flight Directions for All Birds (all birds = 100%)

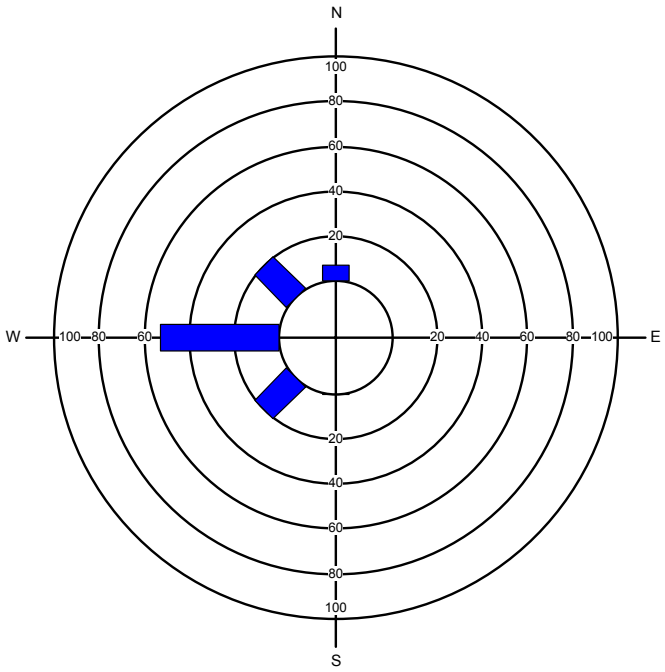


At Brother Islands, 67% of black-crowned night-herons were observed flying south west. At Hoffman, 53% were observed flying west. Hoffman seems to have more dispersion in its flight lines.

Brother Islands, Flight Directions, BCNH (BCNH = 100%)

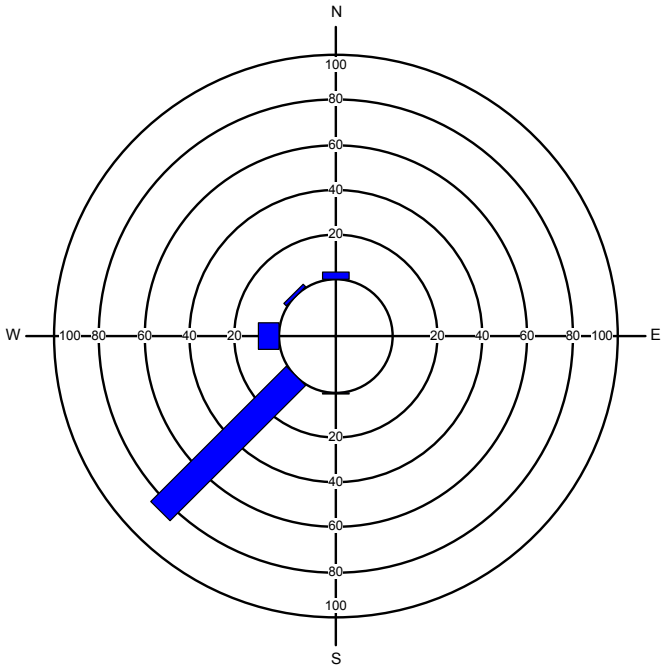


Hoffman Island, Flight Directions, BCNH (BCNH = 100%)

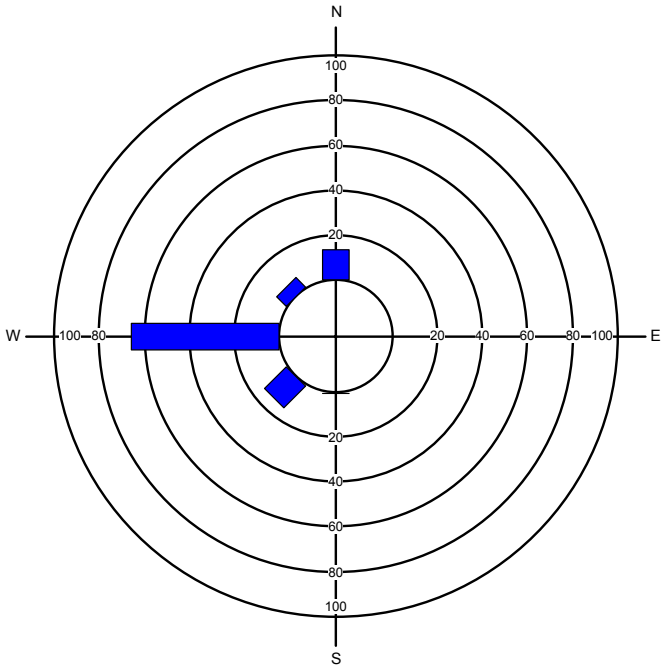


At Brother Islands, 85% of great egrets were observed flying south west. At Hoffman, 66% were observed flying west. Hoffman seems to have noticeably more dispersion in great egrets' flight lines. This finding is even more pronounced for snowy egrets.

Brother Islands, Flight Directions, GREG (GREG = 100%)



Hoffman Island, Flight Directions, GREG (GREG = 100%)



5. Flight Lines and Possible Foraging Areas: **Wading bird flight lines observed at Brother Islands and Hoffman colonies and possible foraging areas.**

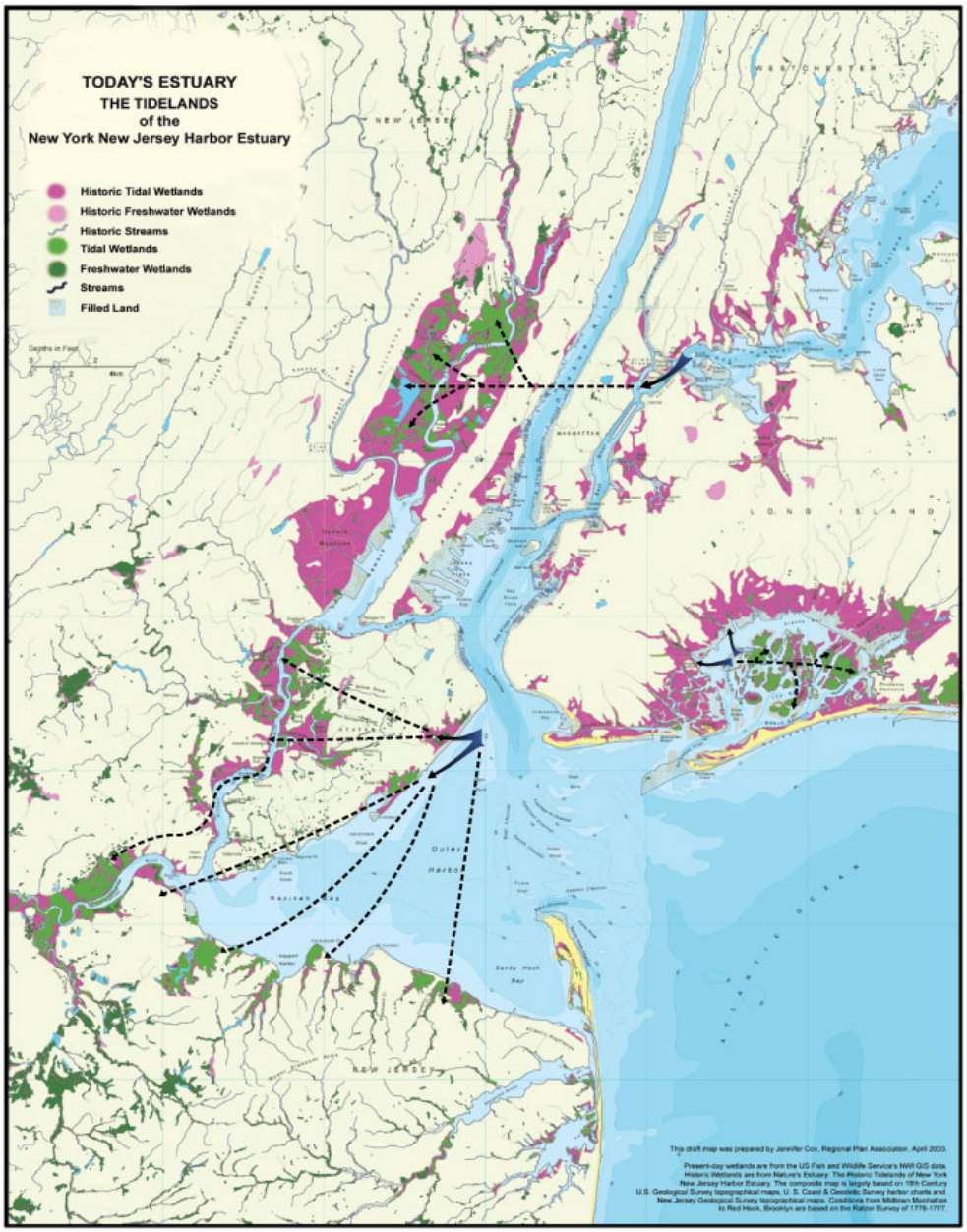


Image: http://www.rpa.org/projects/openspace/maps/draft_todaysestuary.jpg
Special thanks to Jeff Frezoco for drawing in the flight lines.

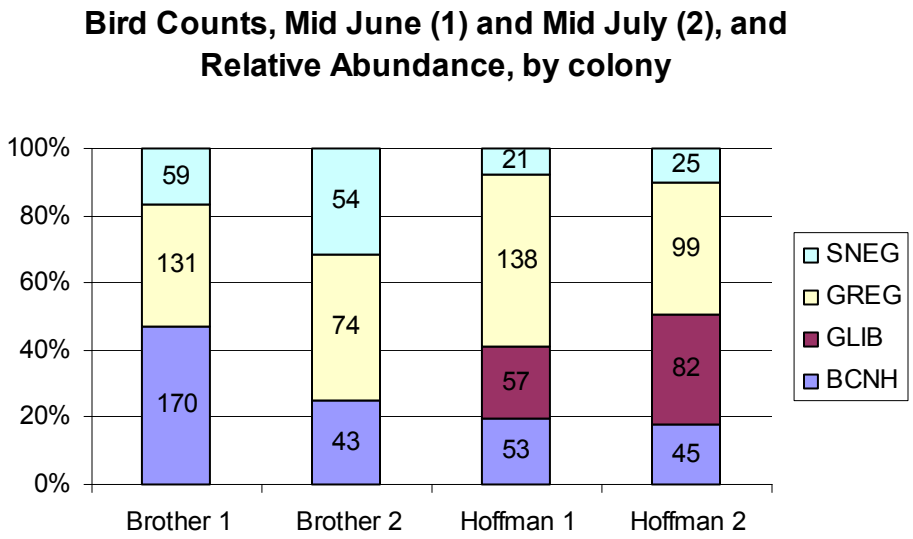
Lines in solid black represent the major flight lines observed during the course of the first and second year of Harbor Herons Shore Monitoring (summer of 2004 and 2003). Dashed lines represent *pojected* flight lines. All three major wading bird colonies in New

York Harbor are represented in this map with Brother Islands at the top, Hoffman in the bottom left and Canarsie Pol in the bottom right.

Specifically for Brother Islands colony, data gathered during the 2003 Shore Monitoring Program showed birds flying over Mill Rock Island on an East West path, which is why the black line (which turns red) bends sharply at that point.

The map above seems to suggest that birds from each colony mostly forage in locations unique to their colony: Flight lines for Brothers colony show most birds flying south west and then west towards NJ Meadowlands (opposite directions on the return flight). Flight lines for Hoffman colony show most birds flying West and South west towards Staten Island and surrounding areas. Flight lines for Canarsie Pol suggest that most birds fly east into Jamaica Bay.[3] The data from the foraging grounds also suggests that birds from other colonies do not forage outside their unique areas, for instance, no ibis have been observed in the NJ Meadowlands, suggesting that ibis from Hoffman Island do not fly up to the foraging areas of Brother Islands (glossy ibis were breeding at Hoffman Island but not at Brother Islands during 2004). The colony of Canarsie Pol has been added here in order to highlight the fact that most birds from that colony do not fly towards the foraging areas of Brother Islands and Hoffman, and therefore are not relevant to the analysis in any significant way.

6. Species Composition: **Total and relative bird abundance at beginning (1) and midpoint (2) periods for each colony** (based on the counts of birds flying in and out of the colony and not nesting counts).



[3] Anecdotal data as well as the following inference process were used to arrive at this conclusion: given that the numbers seen during monitoring (from the location to the West of the colony) were very small, it is very likely that most of the birds flew in the opposite direction, into the Bay.

Glossy ibis were only present at the Hoffman colony. This species significantly increased in numbers from Period 1 to Period 2, while all other species decreased in numbers or increased only slightly.

7. Regressions **The regressions test the hypothesis that outward-bound flight did not differ among colonies, weeks in the season, morning or evening sessions, bird species, cloudy or clear skies, wind speeds and wind directions, air temperatures, tide levels and flooding or ebbing tides for tides at the colonies or at the suspected foraging grounds.**

Regression 1: Tides included height and direction at the colonies.
Regression results of a linear probability model in which outward-bound flight (from the colony) is the dependent variable and abiotic conditions are the independent variables.

Number of obs = 1433
F(11, 1421) = 15.61
Prob > F = 0.0000
R-squared = 0.1078
Adj R-squared = 0.1009
Root MSE = .46807

Dependent Variable = Outward flight from colony (in_out)

Variables	Coef.	Std. Err.	P>|t|
Brothers Isl. Colony (brother)	**-0.225 * * ***	0.043	**0.000**
Week in the season (week)	**-0.015**	0.017	**0.351**
Evening session (obs_time)	**-0.174 * * ***	0.051	**0.001**
Great Egret (greg)	**-0.238 * * ***	0.029	**0.000**
Snowy Egret (sneg)	**-0.160 * * ***	0.037	**0.000**
Black-crowned Night-Heron (bcnh)	**(dropped)**		
Clouds over colony (cloud)	**-0.089 * * ***	0.034	**0.010**
Wind speed (wind)	**-0.009 * ***	0.004	**0.035**
Wind from NW, W, SW (wind_w)	**0.113 ***	0.060	**0.059**
Air temperature in shade (temp)	**0.001**	0.006	**0.907**
Tide height at colonies (td)	**0.012**	0.024	**0.603**
Tide direction at colonies (td_dir)	**0.023**	0.039	**0.557**
Constant	**1.003**	0.161	**0.000**

Significance level: slightly significant: *= 0.05<P<0.1, significant: **=0.01<P<0.05, very significant: ***=P<0.01

Regression 2: Tides include height and direction at suspected foraging areas.
Regression results of a linear probability model in which outward-bound flight (from the colony) is the dependent variable and abiotic conditions are the independent variables.

Number of obs = 1433
F(11, 1421) = 15.84
Prob > F = 0.0000
R-squared = 0.1092
Adj R-squared = 0.1023
Root MSE = .46769

Dependent Variable = Outward flight from colony (in_out)

Variables	Coef.	Std. Err.	P>|t|
Brothers Isl. Colony (brother)	**-0.234 * * ***	0.034	**0.000**
Week in the season (week)	**-0.009**	0.016	**0.575**
Evening session (obs_time)	**-0.138 ***	0.080	**0.085**
Great Egret (greg)	**-0.245 * * ***	0.030	**0.000**
Snowy Egret (sneg)	**-0.168 * * ***	0.037	**0.000**
Black-crowned Night-Heron (bcnh)	**(dropped)**		
Clouds over colony (cloud)	**-0.078 * ***	0.036	**0.028**
Wind speed (wind)	**-0.005**	0.004	**0.255**
Wind from NW, W, SW (wind_w)	**0.089**	0.059	**0.127**
Air temperature in shade (temp)	**0.002**	0.005	**0.682**
Tide height at foraging area (td_f)	**0.048 ***	0.028	**0.085**
Tide direction at foraging area (td_f_dir)	**0.037**	0.076	**0.624**
Constant	**0.814**	0.190	**0.000**

Significance level: slightly significant: *= 0.05<P<0.1, significant: **=0.01<P<0.05, very significant: ***=P<0.01

The regressions show that the likelihood of outward-bound flights differed significantly among colonies, morning and evening sessions, bird species, and cloudy and clear skies; wind speeds, wind directions and tide level at suspected foraging grounds were also

found to be significant to slightly significant. Signs were negative for all of the above except for wind direction and tide level at suspected foraging grounds.

Regression 1 and 2 underscore trends already identified in the paper: outward-bound flight (dependent variable) was 22-23% less likely to occur at Brother Islands colony (very significant), 14-17% less likely to occur during evening sessions (very significant, Reg. 1; slightly significant, Reg. 2), 24% less likely to occur if species was great egret and 16-17% less likely to occur if species was snowy egret (both very significant). Regarding other conditions, both regressions suggest that outward-bound flight was 8-9% less likely when sky was cloudy over the colonies (very significant, Reg. 1; significant, Reg. 2). Regression 1 suggests that outward-bound flight was 1% less likely when winds were apparent (wind speeds ranged from 0 to 22 mph) (significant). Regression 1 also suggests that outward-bound flight was 11% more likely when winds were blowing from south west, west, and north west ("headwinds"). This surprising result, though, is only slightly significant in Reg. 1 and not significant in Reg. 2.

Regarding tide data, regression 1 finds both tide level and tide direction at colonies to be *insignificant*. Interestingly, regression 1 results hold when tide variables are dropped entirely from the regression. When tides at foraging grounds are added to the regression, in regression 2, trends associated with evening and morning observations, cloudiness, wind speeds, and wind direction become less significant or not significant at all. Tide level, however, becomes slightly significant and is associated with a 5% likelihood of outward flight. These results suggest that tide cycles, both at the colonies and suspected foraging grounds, do not greatly affect outward-bound flights.

Air temperature in the shade and week in the season were not even slightly significant in either regression.

When regression 1 was run separately for Brother Islands and for Hoffman colonies, many of the trends persisted with a few notable exceptions: week in season had a beta coefficient of about -10% and significant for each colony. Wind from the west was about +30% and significant for each colony. Results for cloud coverage differed among colonies, with +25% at Hoffman (not significant) and -25% at Brothers and very significant.

Regarding cloud coverage, most of the "cloudy day" observations were disproportionately concentrated at Brother Islands colony as the table below makes clear:

	Not Cloudy	Cloudy	Total
Brother	582	327	909
Hoffman	444	80	524
Total	1026	407	1433

This suggested that the In/Out flight patterns described earlier could merely be the result of monitoring taking place during cloudy days at one colony (Brothers) and during clear days at the other (Hoffman). Furthermore, as shown in the table below, cloudy days were

evenly distributed across evening and morning sessions at Brother Islands. This means that if cloudiness did affect In/Out flight patterns, then both morning and evening sessions would be affected.

Brothers:

	Evening	Morning	Total
Not Cloudy	230	352	582
Cloudy	157	170	327
Total	387	522	909

Hoffman:

	Evening	Morning	Total
Not Cloudy	307	137	444
Cloudy	9	71	80
Total	316	208	524

However, the In/Out patterns found earlier were found to persist when tabulating the In/Out flight data using only clear skies observations (dropping cloudy skies) for great egrets and snowy egrets[4]. Birds were still found to mostly enter Brother Islands in the evening but both enter and leave in equal numbers at Hoffman and mostly leave Hoffman in the morning but both enter and leave in equal numbers at Brother Islands (Table 3). This suggests that cloudiness could not be used to explain the inter-colony differences identified earlier.

Table 3. Flights in and out of colonies for great egrets and snowy egrets during morning and evening sessions for clear skies only.

Brothers:

	Evening	Morning	
In	125	128	253
Out	37	182	219
Total	162	310	472

Hoffman

	Evening	Morning	
In	99	24	123
Out	127	93	220
Total	226	117	343

[4] Ibis are dropped since they are only present at Hoffman; black-crowned night-herons are dropped here since they were present at different relative abundances at each colony (Kerlinger 2004). The trends outlined above persist even if these measures are not taken.

Discussion:

As presented in the results section, Morning/Evening averages, In/Out flight averages, In/Out flight activity, flight directions at the colonies, and the regressions all point to significant differences in wading bird flight activity among Brother Islands and Hoffman colonies. These differences are reflected in the regression analysis as well, with outward-bound flights 22-23% less likely at Brother Islands compared to Hoffman ($P<0.001$), controlling for all other variables.

Why such differences should exist in wading bird flight activity among colonies located in the same harbor is not obvious. Some possible hypotheses are considered below:

1. Asynchronous breeding phases among colonies: It is possible that the breeding cycle started earlier on one colony compared with the other. The data doesn't seem to support this theory, though. First, the differences in In/Out flight patterns were noticed on both islands already in the first week when both were monitored (week 2). Second, the breeding season seemed to come to an end at about the same time at both colonies.
2. Differences in abiotic conditions at colonies: Since both colonies were monitored a day apart during the same time of day each week (during either morning or evening sessions), general abiotic conditions, such as cloud coverage, precipitation, wind speeds and wind directions, air temperature, and tide patterns, would have been somewhat similar for both colonies. However, as shown in the regression section, cloudiness was found to be a condition associated more with Brother Islands. Despite this, the data clearly suggests that differences identified earlier cannot be explained by this abiotic condition alone (Table 2).
3. Tides were analyzed more in depth, with tide patterns at both colonies and possible foraging grounds examined. In both cases (Reg. 1 and 2), tides were not found to be an important factor in explaining inter-colony differences.
4. The location of foraging areas is useful in explaining some of the differences among the colonies, mainly those relating to the relative dispersion of flight directions across species in each colony. The reason that Hoffman seems to have a relatively higher dispersion in flight directions is probably due to the fact that the foraging grounds associated with Hoffman are more dispersed relative to those of Brother Islands (Map in section 5). However, the distance from these foraging grounds to each colony are roughly the same, and given the speed in which the birds fly, any differences in distance don't seem to be sufficient to explain the other differences among the colonies.

There are two additional explanations for the differences among the colonies and both have to do with the colonies' species composition and geography:

1. Glossy Ibis: This species was only present at Hoffman colony. It is also documented to be very territorial and aggressive towards other wading birds including its own species (Netherton 1994). If this species can demand priority in leaving and entering the colony over the other species of day birds, it could explain why flight activity was lower during morning sessions at Hoffman compared with Brother Islands. It could also explain why, at Hoffman, the other species of day birds (great egrets and snowy egrets) were relatively less abundant in the morning sessions compared with the evening sessions while the opposite was true for ibis, which were relatively more abundant during morning sessions. Finally, as shown in the species composition section, ibis is the only species which saw its numbers increase significantly, both in relative terms and in total numbers, from the early to midpoint period in the season while the other species declined in numbers or remained roughly the same. This suggests that ibis did have a certain measure of dominance at Hoffman.

2. Cormorants: This species was present at both colonies, though its spatial distribution and absolute numbers differed among colonies. In Brother Islands, this species was located entirely on South Brother and numbered 350 nesting pairs (Kerlinger 2004). South Brother also included an additional 381 nesting pairs of wading birds (Kerlinger 2004). At Hoffman colony, on the other hand, only 35 nesting pairs of cormorants were present on Hoffman (which included 500 nesting pairs of wading birds) with most of the cormorants nesting on the nearby Island of Swinburne (Kerlinger 2004). Dividing South Brother and Hoffman's total bird populations (including cormorants) by the area of each island in order to find each island's bird-density shows the density at South Brother to be twice that of Hoffman's with 100 birds/acre and 50 birds/acre, respectively.

   The crowded conditions on South Brother coupled with the fact that cormorants were the abundant species on that island, could have caused other day birds (i.e. great egrets and snowy egrets) to roost off the Island in larger numbers compared to Hoffman. In this case, it is likely that many of the wading birds would not return to the colony until later in the morning of the following day in order to replace the parent bird which remained on the Island. This could explain why Morning/Evening flight averages were higher in the evening at Hoffman compared to Brothers – at Hoffman, the activity was more spread-out throughout the day, while at Brothers it was more heavily concentrated in the late morning. More birds roosting at the foraging grounds would also explain why evening In/Out flight averages were relatively low. Since morning outward-bound flights where now delayed at South Brother (since the birds were arriving from their off-island roost, as well as allowing cormorants to leave the Island first) this could also explain why morning In/Out flight averages at Brother Islands were about equal, while at Hoffman they were mostly outward-bound. Finally, if cormorants had a precedence-in-entry in the evening as well, at this could explain why In/Out flight activity increased at Brothers as the evening sessions progressed but decreased at Hoffman.

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