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ABSTRACT

INVESTIGATING THE NIGHTTIME DEPARTURES OF GLAUCOUS-WINGED GULLS
(*LARUS GLAUCESCENS*) AND THE ROLE OF SOCIAL FACILITATION

By

Devon Leigh McClain

Chair: Gordon Atkins, Ph.D.

ABSTRACT OF GRADUATE STUDENT RESEARCH

Thesis

Andrews University

College of Arts and Science

Title: INVESTIGATING THE NIGHTTIME DEPARTURES OF GLAUCOUS-WINGED GULLS (*LARUS GLAUCESCENS*) AND THE ROLE OF SOCIAL FACILITATION

Name of researcher: Devon Leigh McClain

Name and degree of faculty chair: Gordon J. Atkins, Ph.D.

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Daytime behaviors and occupancy patterns of Glaucous-winged Gulls (*Larus glaucescens*) have been described and can be mathematically predicted based on environmental factors. However, little is known about the nighttime behaviors of Glaucous-winged Gulls. I used trail cameras to study the daytime and nighttime colony occupancy patterns of Glaucous-winged Gulls on a breeding colony on Protection Island, Washington, USA. Early in the breeding season gulls desert the colony *en masse* during nighttime even after some gulls have initiated clutches. Using acoustic recording units to identify an acoustic cue that signals the onset of the coordinated nightly departures from the colony, I found that five to ten minutes prior to the nighttime departures the gulls engage in a bout of synchronous extended long-calling. The departing gulls form two large rafts at night to the north and south of the island, both of which get closer to the colony as the season progresses. As more gulls initiate clutches, a switch occurs such that all gulls remain overnight on the colony even though a majority of them have yet to

initiate clutches. The first gulls to initiate clutches influence the transition from leaving to remaining on the colony at night through social facilitation.

Andrews University
College of Arts and Sciences

INVESTIGATING THE NIGHTTIME DEPARTURES OF GLAUCOUS-WINGED GULLS
(*LARUS GLAUCESCENS*) AND THE ROLE OF SOCIAL FACILITATION

A Thesis
Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

by
Devon Leigh McClain
2020

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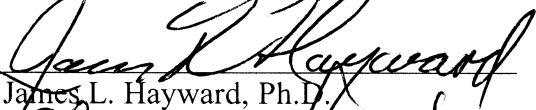
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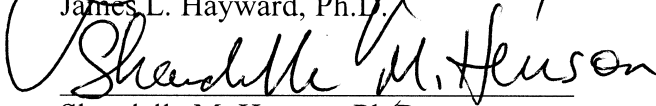
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LIST OF ABBREVIATIONS

| | |
|-----|-------------------------|
| ARU | Acoustic recording unit |
|-----|-------------------------|

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CHAPTER 1

INTRODUCTION

Gulls are important model organisms for studying environmental factors in marine ecosystems. They are relatively large and accessible organisms, multi-year breeders, and sensitive to changing environmental conditions, making them useful indicator species for the marine environments in which they spend much of their time (Hayward et al. 2014, Blight et al. 2015, Davis et al. 2017). Glaucous-winged Gulls (*Larus glaucescens*) breed in the northern Pacific, from the Aleutians (Alaska) to northern Oregon and across the Pacific in northeast Russia and neighboring lands (Ebels et al. 2001, Hayward and Verbeek 2020). They are capable of hybridization with other gull species where distributions overlap (Scott 1971, Bell 1997, Ebels et al. 2001).

Glaucous-winged Gulls raise up to three chicks in a breeding season (Megna et al. 2014, Hayward and Verbeek, 2020). The chicks are raised on offshore islands, where these gulls typically form colonies (Hayward and Verbeek 2020). They feed on a variety of food sources depending on location and abundance (Moyle 1966, Hayward and Verbeek, 2020).

Mathematical modeling, using environmental factors as independent variables, can be used to reliably predict diurnal habitat occupancies by Glaucous-winged Gulls. During high tide, late in the season, and during low solar elevation the gulls are more likely to be on the colony (Henson et al. 2004, Moore et al. 2008). Hayward et al. (2014) demonstrated a negative relationship between high sea surface temperature and egg cannibalism in on Glaucous-winged Gulls. In particular, they showed that an increase of 0.1°C is associated with a 10% increase in the odds that a given egg was cannibalized (Hayward et al. 2014). This is attributed to their normal prey moving to deeper, cooler waters and out of reach to the gulls (Hayward and Verbeek

2020, Surman and Nicholson 2009). Cannibalism can lead to a decrease in the gulls' reproductive success and ultimately to a decrease in the population (Stenseth et al. 2002, Moncrieff et al. 2013, Hayward et al. 2014). In response to increased cannibalism, gulls ovulate and lay eggs synchronously, decreasing the chance that a given egg will be cannibalized on a given day (Henson et al. 2010, Henson et al. 2011).

Interspecific predation and disturbances have been evaluated as well. Bald Eagles (*Haliaeetus leucocephalus*) prey on eggs, chick and adult gulls and often disturb the colony on Protection Island, Washington (Galusha and Hayward 2002, Hayward et al. 2010, Cowles et al. 2012). Henson et al. (2019) demonstrate a negative correlation between the increases in eagles and the number of gulls breeding on this colony.

Despite many studies on the diurnal behaviors of the gulls, only a few studies have evaluated their nighttime behaviors (Hayes and Hayward 2020). Franklin's Gulls (*Leucophaeus pipixcan*) overnight on water near the colony and, when eggs are present in nests, the owners remain with the eggs. Those that do not have eggs roost on open-water near the colony but are not tethered to the colony itself (Burger and Gochfeld, 2020). Herring Gulls (*Larus argentatus*) roost near or on their nests during the breeding season and their sleeping behaviors have been evaluated (Tinbergen 1960, Amlaner et al. 1981, Amlaner 1983). Outside of the breeding season, Herring Gulls roost as large groups in open areas with substantial open space between the group and potential predators, sometimes flying long distances from daily loafing sites to find areas that match this description (Schreiber 1967).

In this project I asked 1) if there is seasonal variation of the Glaucous-winged Gulls' occupancy of the colony during both day and night, 2) if an auditory cue might serve as the trigger for synchronized evening departures, 3) if there is seasonal variation in the location of

nighttime rafting, and 4) if gulls that lay the first clutches are more likely to leave later from the colony in the evening than their neighbors and arrive to the colony earlier in the morning.

CHAPTER 2

METHODS

Data for this study were collected on a gull breeding colony on Violet Point, Protection Island National Wildlife Refuge in Jefferson County, Washington, USA (Figure 1). This colony includes Glaucous-winged Gull x Western Gull (*Larus occidentalis*) hybrids. Previous research has identified the gulls on this colony to be more closely related to Glaucous-winged Gulls than to Western Gulls (Moncrieff et al. 2013, Megna et al. 2014). Because of this, we have chosen to call the residents of this breeding colony Glaucous-winged Gulls. The colony is located on a gravel spit that extends southeast off the island and is home to ~5000 gulls (Henson et al., 2007).

Evaluating Seasonal Variation of Nighttime Occupancy

Occupancy was calculated from images captured by infrared trail cameras (Bushnell Trophy, model #119736). The cameras were mounted 1–1.5 m above the ground on posts at 8 locations: 3 in breeding locations and 5 in non-breeding locations in 2017 (Figure 1A) and in 4 breeding locations in 2018 (Figure 1B). The cameras took still images at the top of the hour, every hour, both day and night from April 4–June 13, 2017 and April 17–June 7, 2018. The number of gulls visible in the field of view in the nighttime images were tallied for each image. Due to the limitations of infrared illumination, the field of view for these cameras was less than for the daytime images. To control for this, I counted only the gulls present in the daytime images that were located within the portion of the image equivalent to the illuminated area of the nighttime images.

Raster plots were created to show the seasonal variation of the hour-by-hour occupancy for breeding and non-breeding locations in 2017. The size of each dot reflects the occupancy at

that time. Raster plots for two adjacent breeding areas (Marina Colony East and Marina Colony West) were constructed for both 2017 and 2018 to determine if overall trends in occupancy occur in both years. To synthesize the complete data set spanning both years, I calculated monthly average occupancies for every hour of the day for the months of April, May, and June.

Evaluating Acoustic Cues Preceding Nighttime Departure

Two *Swift* audio recording units (ARUs) were mounted 1 m off the ground on posts at two breeding locations in the gull colony: one at the junction between camera locations Marina Colony East and Marina Colony West, and one near the South Beach (Figure 1B). The acoustic recording units were programmed to run from 1800–2400 hr from April 8–11, 2019. The timing and extent of gull movements and eagle disturbances were observed from the bluff during the same time as the audio recording units were active. These observations allowed us to identify and evaluate various events on the audio recordings. A second set of data was recorded from the same units in the same location from April 12–18, 2019. For this data set, the audio recordings were continuous and there were no corresponding observations made from the bluff. Departure and return times for these recordings were determined by the total absence of gull noise in evening hours and the resumption of gull vocalizations in the early morning.

All recordings were evaluated using RavenLite 2.0 (Center for Conservation Bioacoustics, Cornell Lab of Ornithology). The mean sound intensity was evaluated in 40-min increments and plotted on a 24-hour axis. In addition, the mean sound intensity was re-evaluated in 5-min intervals for 30 min prior to departures. Using the time stamps from the visual observations made from the bluff, I searched for auditory signatures (temporal and/or spectral) that may have accompanied nighttime departures as well as for departures caused by eagle disturbances.

Evaluating Where Departing Gulls Go at Night

A hand-held digital infrared camera (Bestguarder WG-50) was used from an observation point on the bluff to follow departing gulls in April and May 2016-2018 (Figure 2). The rafts of gulls that form offshore were either photographed or their approximate location was triangulated using the sound produced by the rafting gulls and compass readings from two locations on the bluff. The calculated location of the raft was then plotted relative to a fixed reference point on Violet Point, in order to calculate the approximate angle and distance from the colony.

Evaluating the Transitions in Occupancy

To determine if nightly departures of the gulls from the colony were influenced by the presence of eggs in the nests, the occupancy at 0300 hr (a time most gulls are consistently gone from the colony) from the 2017 trail camera data described above was compared to egg census data collected from the whole colony from May 23–June 13, 2017. Egg census data were collected by daily walking through the sample plots (at approximately 1800 hr) and locating all nests containing eggs. Nests with clutch initiations were marked with a numbered post. The eggs were labeled in alphabetical order as they occurred (A for the first, B for the second, etc.) with permanent marker. The persistence and losses of clutches were recorded until the end of the census. Egg census methodology is described in detail in Atkins et al. (2015).

To determine if the clutch initiation influences the owners' departures at night and arrivals in the morning infrared trail cameras were positioned near the first 16 nests within which clutches had been initiated. These trail cameras were programmed to take photographs every minute from 2130–0500 hr. The total number of gulls in the field of vision at 2130 hr was counted and used for a maximum occupancy before departure. Correction for differences between nighttime and daylight images followed the procedures described above. The images

were then advanced, frame by frame, until the first frame in which the resident gull of the nest was absent. The previous image was used to count the number of gulls present just before the resident gulls left. This number was used as a maximum number of gulls that might have stayed after the resident gulls left; with 1 min resolution we cannot be sure when the resident gull left relative to the remaining gulls in that frame. This number was then compared to the number of gulls present at 2130 hr and the difference between them plus one (to account for the resident gull) was used to calculate the number of gulls that left before the resident gull.

A similar procedure was used to evaluate the return of gulls in the morning. The frames from overnight were advanced until the first frame in which the resident gull was present. The number of gulls in that frame was counted to determine how many gulls may have arrived before the resident gull. This number was then compared to the total number of gulls counted on the colony in the field of view at 0500 hr. The difference plus one was used to calculate the number of gulls that returned after the resident gull. Chi-Square analysis was used to test whether these results were significantly different than what was to be expected if gulls left from and arrived back to the colony randomly, and if there were changes as the season progressed.

CHAPTER 3

RESULTS

Seasonal Variation of Nighttime Occupancy

Although there were fewer gulls in non-breeding areas (Figure 2A–C) than in breeding areas (Figure 2D–F), gulls were present on the colony during the day but they were absent at night for approximately 8–9 hr throughout the early portion of the breeding season. As the season progressed, the duration of the time away from the colony at night decreased and became more variable; some nights more gulls stayed longer on the colony compared to the following nights until gulls consistently remained throughout the night. This pattern of presence and absence occurred across all camera locations with more variability occurring in the marina than in any other non-breeding or breeding area. Occupancy recorded from two different breeding seasons (Figure 2D,E from 2017; Figure 2G,H from 2018) showed no clear differences between years. The raster plots from breeding areas show lower occupancies during some parts of the day compared to others, and these periods shifted slightly each day represent gulls leaving for feeding during low tides (Moore et al. 2008).

When the occupancy counts for all breeding and non-breeding locations were compared by month (Figure 3) there was a clear window in which the gulls were absent at night in April. That window of absence narrowed in May as gulls began remaining overnight on the colony later in the month. By June, all the gulls, both at breeding and non-breeding locations, remained through the night (Figure 3). Occupancy increased during daylight hours proceeding departures, particularly in April. This trend was most obvious between 2000–2100 hr in non-breeding locations (Figure 3B).

Acoustic Cues Preceding Nighttime Departures

During the gulls' absence at night, the average ambient sound intensity on the colony was low and varied between -90 and -86.5 dB/FS. When gulls arrived back in the morning, the average sound intensity increased to an average of -59.9 dB/FS (Figure 4A). While gulls were present on the island during the daylight hours the average sound intensity ranged between -65.0 and -59.5 dB/FS, with a 3.8 dB/FS increase in the 40-min interval before the nightly departures (Figure 4A). The last 30 min before departure was evaluated in 5-min increments. During the last 5-min interval, which includes when the gulls leave, the sound level was significantly quieter than all other times (Figure 4B; ANOVA with repeated measures, Bonferroni, $p < 0.005$). The 5–10 min and 10–15 min intervals before departure were significantly louder than the others (Figure 4B; ANOVA with repeated measures, Bonferroni, $p = 0.024$ and $p = 0.001$). The remaining intervals were not significantly different from the previous 40-min intervals.

A unique acoustic signature occurred within the colony during the loudest period just before departures. The gulls called more or less synchronously, producing a loud sequence of pulses (~2.5/sec) with harmonics extending beyond 20 kHz and lasting 10-15 sec (Figure 5 A,B). While our recording setup was not designed to evaluate what individual gulls were vocalizing during this group signal, they primarily seemed to be using the long call (Stout et al. 1969, Hayward and Verbeek 2020). This acoustic signal (hereafter referred to as synchronous long call) occurred each night at each recording unit ($n = 8$) 5–10 min before the departures occurred (Figure 5 A,B) and did not occur at any other time during the day. Acoustic signatures prior to eagle disturbances were evaluated to compare to the signal occurring prior to nighttime departures. Eagle disturbances were more synchronous than nighttime departures, with gulls lifting off *en masse*, resulting in an acoustic signature of white noise-like sound that lasted ~2–3

seconds and represents the noise of the gulls' wings during take-off (Figure 5C,D). This acoustic signature always accompanied each eagle disturbance (n=8) and was never observed at any other time of the day. After liftoff, the gulls circled and eventually landed after the eagle threat was over, followed by non-synchronous vocalizations including a variety of calls (long call, courtship begging, yelp) which lasted for a variable amount of time after they settled.

Where Departing Gulls Go at Night

Departures occurred over a period of 1–3 min. Sometimes one massive group lifted off over a course of several seconds, while other nights departures occurred in up to 3 waves. The gulls typically flew in a circle once or twice over the colony, followed by one group flying to the north of Violet Spit to form a raft, while the other group flew off to form a raft to the south of the island (Figure 6). Because of the large number of gulls in the air at one time (~5000 gulls) it was not clear which gulls from the colony chose to move north and which chose to move south. In April, the rafts formed far enough offshore so that their locations could not be pinpointed either visually or by sound. As the breeding season progressed, the rafts formed closer offshore from the colony so that their position could be triangulated or observed directly (Figure 7A-C). The rafts occurred closer to shore each night until the gulls remained overnight on the island (Figure 7D). At times, before the gulls remained on the colony overnight, the marina was used as a transition point; some gulls lifted off and landed in the marina before transitioning into the rafts in the evening (Figure 2B).

The Transition in Occupancy

Early in the breeding season when clutches are first being initiated, all the gulls left the colony at night, even if they had eggs in the nest (Figure 8). Later, when all gulls began remaining overnight on the island, many gulls had not yet begun initiating clutches (Figure 8).

Gulls with clutches were significantly more likely to be of the last gulls to leave during nightly departures; 28 times (40.6%) gulls with clutches were the last to leave the colony (Table 1). Those same gulls with clutches were also significantly more likely to be among the earliest to arrive back from the rafts in the morning; of the 70 morning arrivals recorded, the resident gulls with clutches returned first 48 times (68.6%, Table 1). This tendency intensified over time. Comparing the tendency for gulls that had initiated clutches to depart even later and arrive earlier as the seasons progressed two-way chi-square analysis indicated that the gulls with the first clutches are disproportionally more likely to return to the colony earlier and leave later as the season progresses, $X^2(1, n = 16) = 12.61, p < 0.001$ and $X^2(1, n = 16) = 19.05, p < 0.001$ (Table 2;).

CHAPTER 4

DISCUSSION

This study demonstrates that Glaucous-winged Gulls left the colony at night early in the breeding season. The gulls produced what appeared to be a synchronous long call ~10 min before they left as a group in the evening to form rafts to the north and south of the island. These rafts formed consistently closer to the colony later in the breeding season until all gulls began remaining overnight on the colony, despite many birds having yet to initiate a clutch. Gulls with earlier clutches were more likely to leave the colony later than the others and to arrive back earlier when gulls rafted overnight off-colony.

A number of studies have shown a seasonal effect on daytime behavior of seabirds. Black Guillemots (*Cepphus grylle*), for example, are more likely to be present on the colony at any time than any other alcid species (Ewins 1985, Butler et al. 2020). Black Guillemots typically can be found on the colony in the morning before heading off to feed before returning to the colony in the afternoon during the prebreeding season in Shetland (Ewins 1985, Butler et al. 2020). However, morning occupancy decreases are followed by a pronounced increase in the afternoon colony attendance associated with the incubation period of eggs which reverses once the nestling period begins (Ewins 1985, Butler et al. 2020).

While little is known about Pigeon Guillemots (*C. columba*) outside of the breeding season, these alcids also display seasonal variation in colony occupancy, although it typically varies a great deal as the birds come and go from the colony throughout the day. Both sexes are more likely to be off the colony feeding at low tide, with occupancy increasing in the morning and evening (Ewins 2020). Female Pigeon Guillemots are more likely than males to be absent

from the colony just prior to egg laying, a factor that decreases the overall colony attendance during this time period (Nelson 1987, Ewins 2020).

Grey-faced Petrels (*Pterodroma macroptera gouldi*) also exhibit seasonal variation in colony occupancy. Both breeding and nonbreeding birds return to breeding colonies by the end of March (Ross and Brunton 2002, del Hoyo et al. 2020). They leave the colony entirely for a period before laying in early June, with males being gone ~50 days and females for ~60 days (Ross and Brunton 2002, del Hoyo et al. 2020) and likely includes both breeding and nonbreeding birds. A second exodus from the colony occurs in September and is likely includes only the nonbreeders leaving the colony (Ross and Brunton 2002, del Hoyo et al. 2020) and corresponds with the last of chick hatchings (Ross and Brunton 2002).

Glaucous-winged Gulls exhibit daytime occupancy variation in relation to several environmental factors (Henson et al. 2004, Henson et al. 2006, Moore et al. 2008). Early in the breeding season and at low tide, Glaucous-winged Gulls are often away from the colony (Henson et al. 2004, Moore et al. 2008). As the season progresses and clutches are initiated gulls are more likely to be found on the colony during daylight hours (Henson et al. 2004, Moore et al. 2008).

Few studies have addressed seasonal effects on nighttime behavior, especially outside of laying and incubation season. In several *Larid* species (e.g. Franklin's Gull, Herring Gull), for example, gulls remain on the colony overnight when clutches have been initiated, with non-incubating birds roosting in open water, not on the colony (Schreiber 1967, Burger and Gochfeld 2020).

My results provide an example of conflict behavior mediated by social facilitation. Conflict behavior occurs when two opposing behaviors are at conflict with each other and a resolution must be found (Hinde 1970). Any motion towards one of the goals increases the

probability of that behavior winning out (Hinde 1970). In this case, the “leave” behavior, or going to roost overnight in the rafts, is in conflict with the “stay” behavior to remain to incubate and guard the eggs (Cresswell 1994, Cresswell 2008). Early in the season, the drive to engage in self-protective behavior and leave with the entirety of the colony wins out. As more gulls initiate clutches, the conflict between “stay” and “leave” behavior increases and ultimately reaches a critical tipping point so that social facilitation results in the remaining gulls staying despite not yet having a clutch (Table 2, Figure 8). This transition to staying at night includes loafing or non-breeding gulls, which have no drive or benefit to remain on the colony without eggs to care for. This tendency supports the occurrence of social facilitation.

Where Departing Gulls Go at Night

Many seabirds form rafts on the water near the colony that they leave. Early arrivals to the colony after nocturnal feeding of both Manx Shearwaters (*Puffinus puffinus*) and Black-vented Shearwaters (*P. opisthomelas*) wait in the water near the colony for the rest of the colony before returning to the shore *en masse* (Keitt et al. 2005, Richards et al. 2019). This behavior has been linked to avoidance of diurnal predation.

Similarly, Glaucous-winged Gulls from Protection Island form rafts in water to the north and south of the island after departing from the colony and remain in them through the night until returning in the morning (Figure 7). This behavior is consistent with other species of gulls and provides security from predators (Schreiber, 1967, Good 2020, Winkler, 2020). It is also consistent with other seabirds’ antipredator behaviors (Keitt et al. 2005, Richards et al. 2019). As the season progresses, the rafts begin to form closer and closer to the shores of the colony, though there would be time for the gulls to fly out a farther distance. This response is also consistent with conflict occurring between the tendency to “leave” and the increasing drive to

“stay.” While it is not uncommon for other species to roost near the colony on open-water or in bodies of water adjacent to the colony, even after some birds initiate clutches (Burger and Gochfeld 2020), the positioning of the raft closer and closer to the colony as the breeding season progresses has not been documented in other gull species.

Gulls were not followed on their nightly departures earlier in the breeding season; moreover, their raft locations could not be determined once out of auditory range. The southern raft formed in Discovery Bay, past Diamond Point (~4000 m from Protection Island), according to residents who live at nearby Cape George, while the northern raft has yet to be located during this early stage of the season (R. Anderson personal communication). It might be possible to locate the northern raft by driving by boat to the approximate location and using global positioning technology.

Due to permit restriction on Protection Island National Wildlife Refuge, individual gulls in this study could not be uniquely marked to follow their nighttime flight patterns to determine which gulls chose the north or south rafts. Further research on this topic on a different Glaucous-winged Gull colony which might allow marking gulls may provide more insight.

Acoustic Cues Preceding Nighttime Departures

Gulls are highly vocal birds and communicate through a variety of different types of calls to express different behaviors (Hayward and Verbeek 2020, Atkins et al. 2017). Some calls have even been demonstrated to synchronize the timing of behaviors within the colony, such as copulation calls (Fetterolf and Dunham 1985; Atkins et al. 2017). Therefore, it is not surprising, that an acoustic signal precedes the departures of Glaucous-winged Gulls from the colony and synchronizes this evening departure.

The synchronous long calling of the Glaucous-winged Gulls 5 min before departure was similar to individual long calls in terms of the sequence of pulses (~2.5/sec) and timing between pulses (~0.2–0.3 sec) (Figure 5 A,B). Long calls last ~4–5 sec (Stout et al. 1969, Ashton 1994, Hayward and Verbeek 2020) while the synchronous long calls we recorded lasted 10–15 sec, approximately 2–3 times longer than the long call produced by individual gulls (Figure 5 A,B). The synchronous call of Glaucous-winged Gulls shares fewer similarities with other Glaucous-winged Gull calls.

Due to the nature of the acoustic recording setup, a single gull sitting directly above or below the microphone theoretically could overpower the recording of that portion of the colony and make it sound like the gulls were producing a synchronous long call. This is not likely because the synchronous long call is much longer than a single gull's long call and because it is unlikely that a gull would be positioned under the ARU each evening. Future analysis using several ARUs positioned along the colony could demonstrate the call occurring throughout the entirety of the colony ~10 min before departure.

This synchronous long call, which appears to coordinate the overnight departure in Glaucous-winged Gulls, is similar in function to the “contact calls” used by Ring-billed Gulls (*Larus delawarensis*). Evans and Welham (1985) demonstrated that individual Ring-billed Gulls produce a contact call while in flight when leaving the colony. This is a call that attracts other gulls from off the colony and into the air. However, the contact calls of Ring-billed Gulls act on individuals rather than all colony residents, and contact calls are present immediately preceding or during departure. A second difference is that the synchronous long call takes place ~10 min before the gulls depart rather than during the event itself.

Eagle Disturbances

Bald Eagles have nested on Protection Island since at least the 1920s (Cowles and Hayward 2008). For many years there were relatively few Bald Eagles on the colony to disturb the Glaucous-winged Gull colony, but in the early 1990s the number of Bald Eagles present on the island began to increase (Henson et al. 2019). This coincided with the disappearance of Double-crested Cormorant (*Phalacrocorax auratus*) and Pelagic Cormorant (*Phalacrocorax pelagicus*) colonies on the island and a decline in the population of Glaucous-winged Gulls (Henson et al. 2019).

Besides the synchronous departure at night, eagle disturbances are the only other recorded times in which Glaucous-winged Gulls leave *en masse* from the colony. The acoustic signature preceding eagle departures show no similarities to the evening desertion of the colony (Figure 5 C,D) and could be used to monitor eagle disturbances long term without continual observation. These data could then be used to project the long-term effects of Bald Eagles on the reproductive success of gulls and other seabirds nesting on Protection Island

Conclusion

Glaucous-winged Gulls leave the colony at night early in the breeding season. Later in the season, when some gulls have initiated clutches, all gulls remain on the colony overnight even though relatively few gulls have initiated clutches by that time. A synchronized long call occurs ~10 min before departure and appears to signal the colony-wide decision to depart in the evenings to form rafts on open-water to the north and south of the island. These rafts form closer to the shores of the colony as the season progresses. The first gulls who have initiated clutches are statistically more likely to leave later than their neighbors in the evening and more likely to arrive back earlier in the morning when gulls depart the colony overnight. These gulls with earlier clutches appear to socially facilitate the transition from being absent at night from the

island to remaining through the night. Further evaluation on other Glaucous-winged Gull colonies will be needed to determine if this behavior is geographically specific or species-specific.

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Table 1. Occurrences of the number of gulls that departed before the gulls with clutches departed, and occurrences of gulls that arrived after the gulls with clutches arrived on the first night/morning of clutch initiation and the last night/morning before the switch.

| | n | Observed | Expected | df | X^2 | p |
|---|----|----------|----------|----|---------|-----------|
| First night of clutch initiation | | | | | | |
| Departed before resident | 16 | 167 | 104 | 1 | 38.1635 | p < 0.001 |
| Departed after resident | | 41 | 104 | | | |
| Arrived before resident | 16 | 37 | 116 | 1 | 53.8017 | p < 0.001 |
| Arrived after resident | | 195 | 116 | | | |
| | | | | | | |
| Last night before switch | | | | | | |
| Departed before resident | 16 | 215 | 117 | 1 | 82.0855 | p < 0.001 |
| Departed after resident | | 19 | 117 | | | |
| Arriving before resident | 16 | 9 | 116.5 | 1 | 99.1953 | p < 0.001 |
| Arriving after resident | | 224 | 116.5 | | | |

Table 2. Dependence between departure and arrival relative to resident (clutch initiated) and time in the season

| | Departed later than resident | Departed earlier than resident | <i>p</i> -value |
|-------------------------------------|------------------------------|--------------------------------|-----------------|
| First night after clutch initiation | 41 | 167 | |
| Last night before switch | 19 | 215 | $p < 0.001$ |

| | Arrived earlier than resident | Arrived later than resident | <i>p</i> -value |
|---------------------------------------|-------------------------------|-----------------------------|-----------------|
| First morning after clutch initiation | 37 | 195 | |
| Last morning before switch | 9 | 224 | $p < 0.001$ |

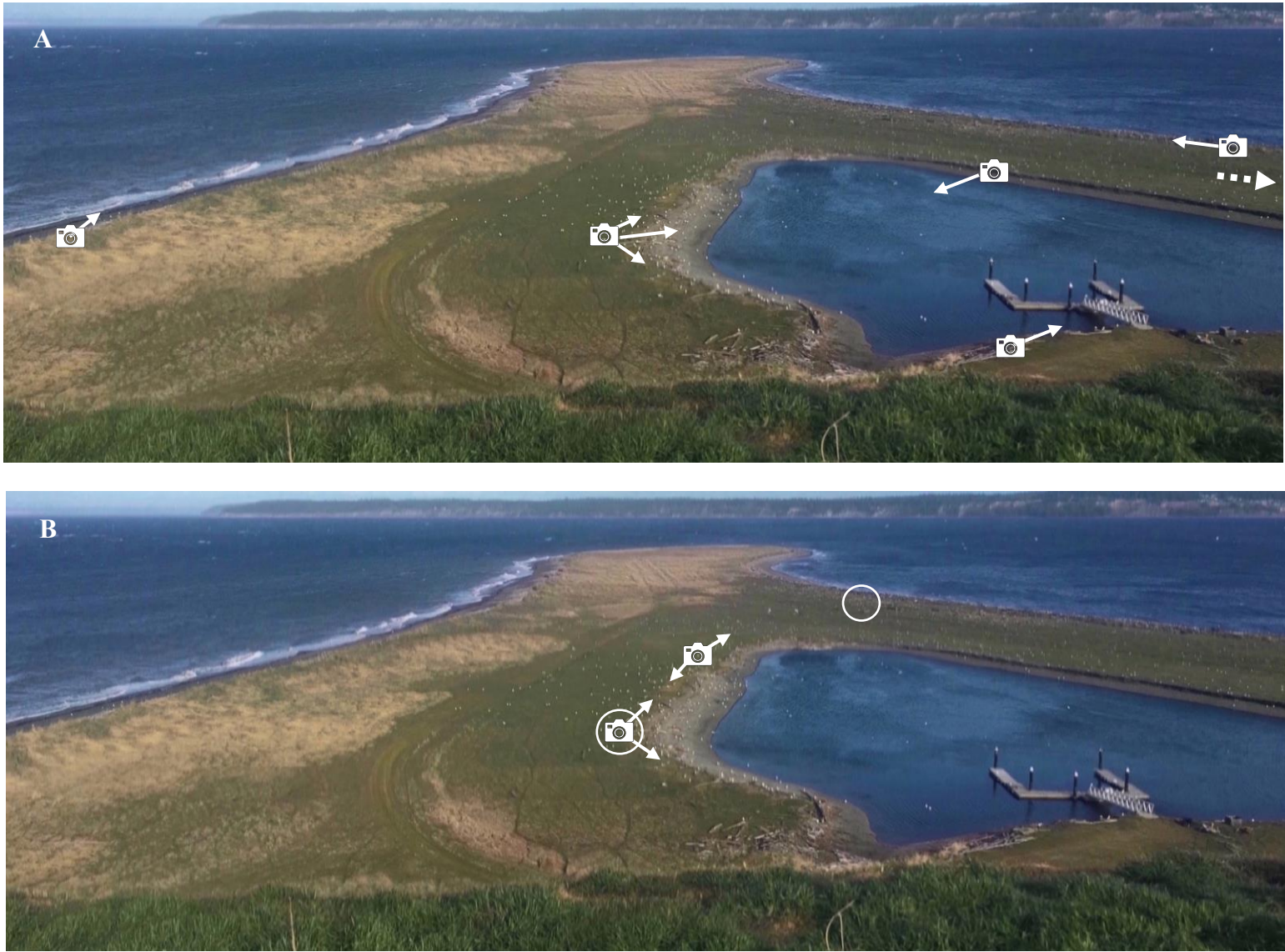


Figure 1. Locations and positions of infrared cameras and audio recording units. Photo of Violet Spit viewed from the observation point in the bluff. Position of infrared camera and audio recording unit (white circles) locations across (A) 2017 and (B) 2018 & 2019. In (A), one camera is located off-image on the jetty, denoted by the lone dotted white arrow. Solid white arrows originating from cameras indicate the direction in which cameras were facing.

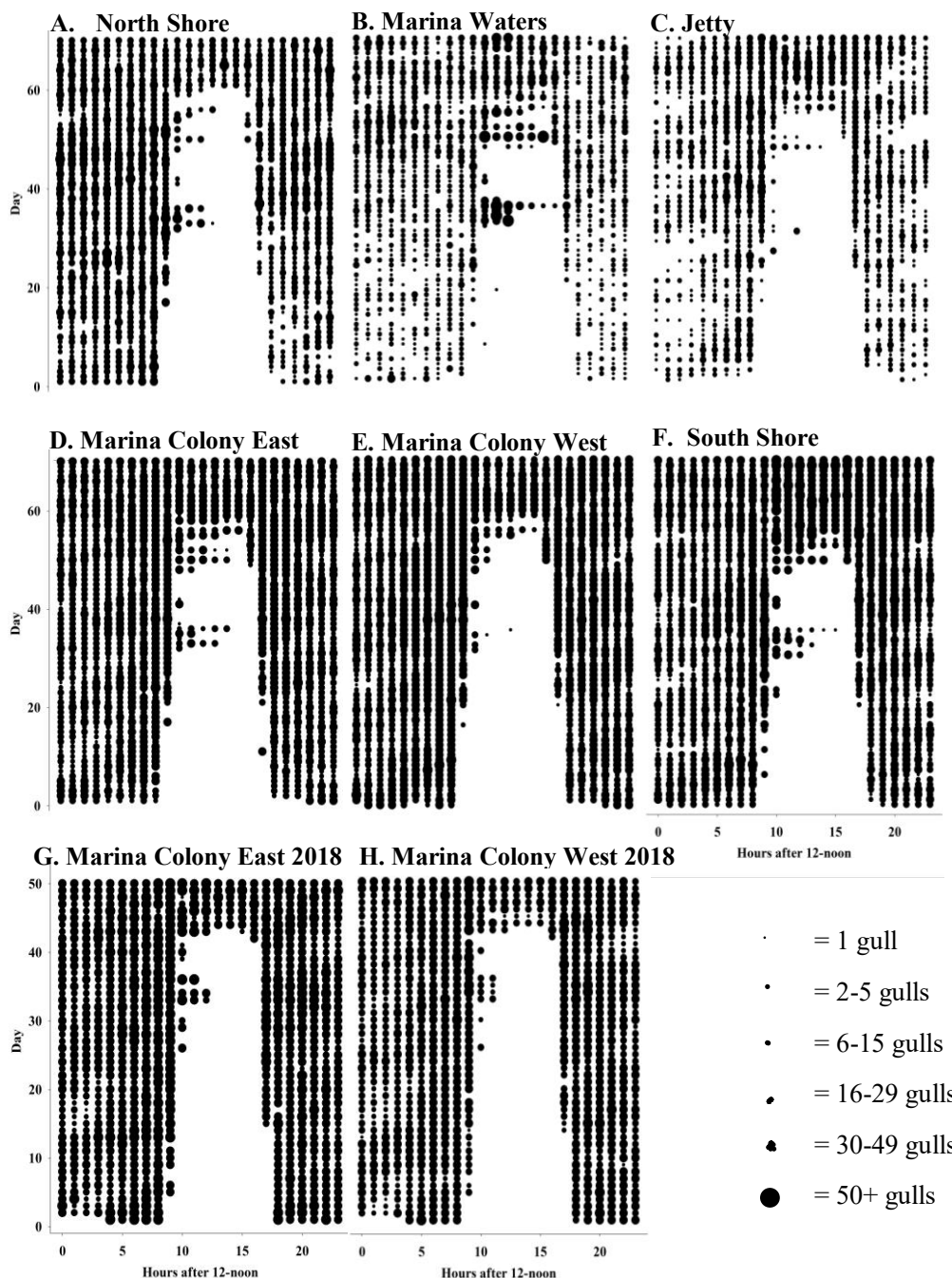


Figure 2. Raster plots of occupancy for nonbreeding and breeding locations on Violet Spit. Raster plots of occupancy for nonbreeding (A-C) and breeding (D-H) locations on Violet Spit. Nonbreeding locations are (A) the north shore, (B) the marina waters, and (C) the jetty. Breeding locations are (D) marina colony east 2017, (E) marina colony west 2017, (F) the south shore, (G) marina colony east 2018, and (H) marina colony west 2018.

Each point represents the presence of gulls at that hour. The size of the point represents a number of gulls; the larger the dot, the more gulls present at that time. Each row represents a day of the project. In order to visualize the window in which the gulls are absent overnight, the Day 1 begins at 12-Noon (0) on the first day of the project and extends until 11 AM of the following day, continuing until the end of the project. Day 1 of the project was April 5 in 2017 (A-F) and April 17 in 2018 (G,H).

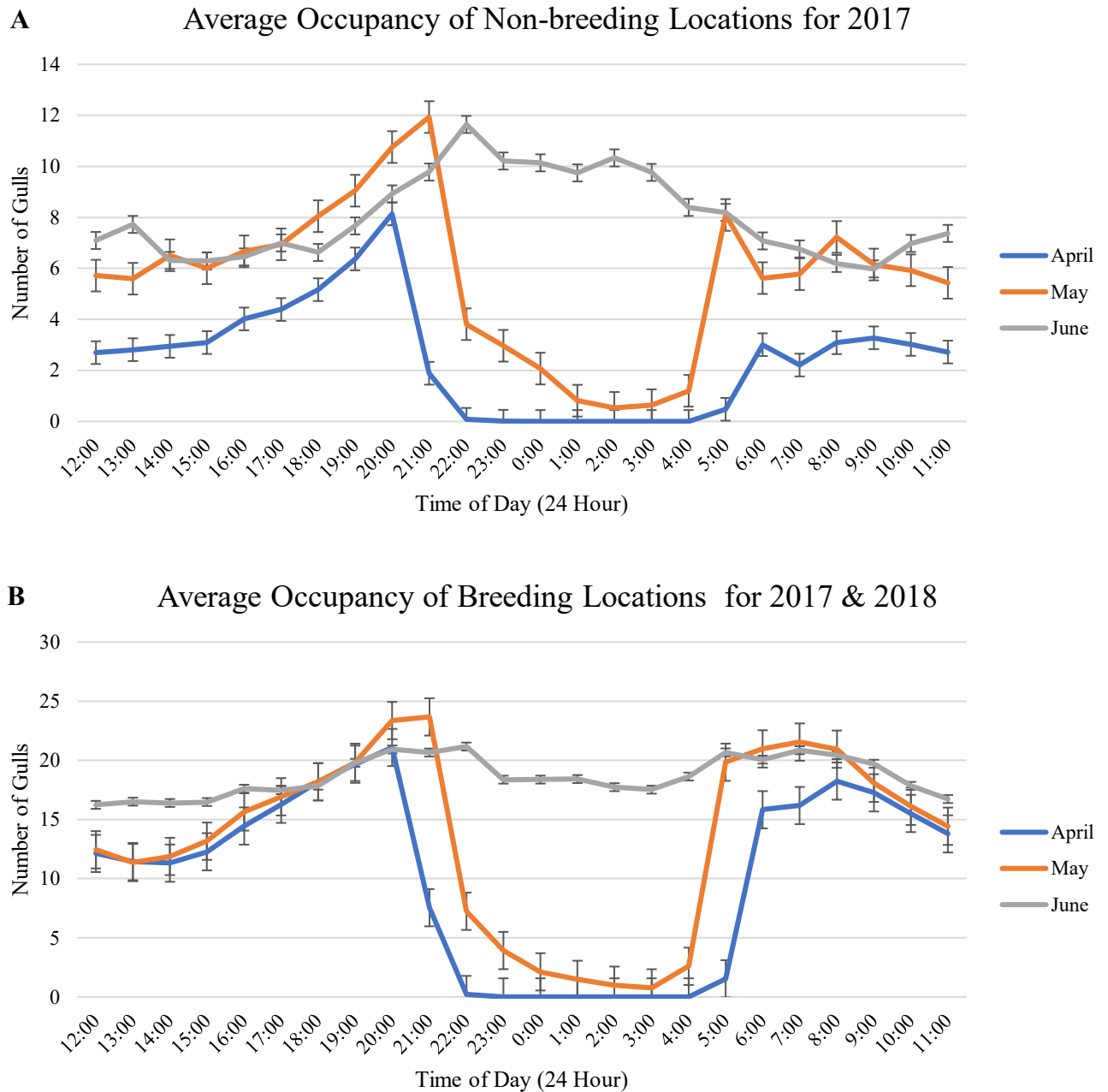


Figure 3. The average hourly occupancy of non-breeding and breeding locations. The average hourly occupancy for (A) non-breeding locations and (B) breeding locations. Error bars represent standard errors.

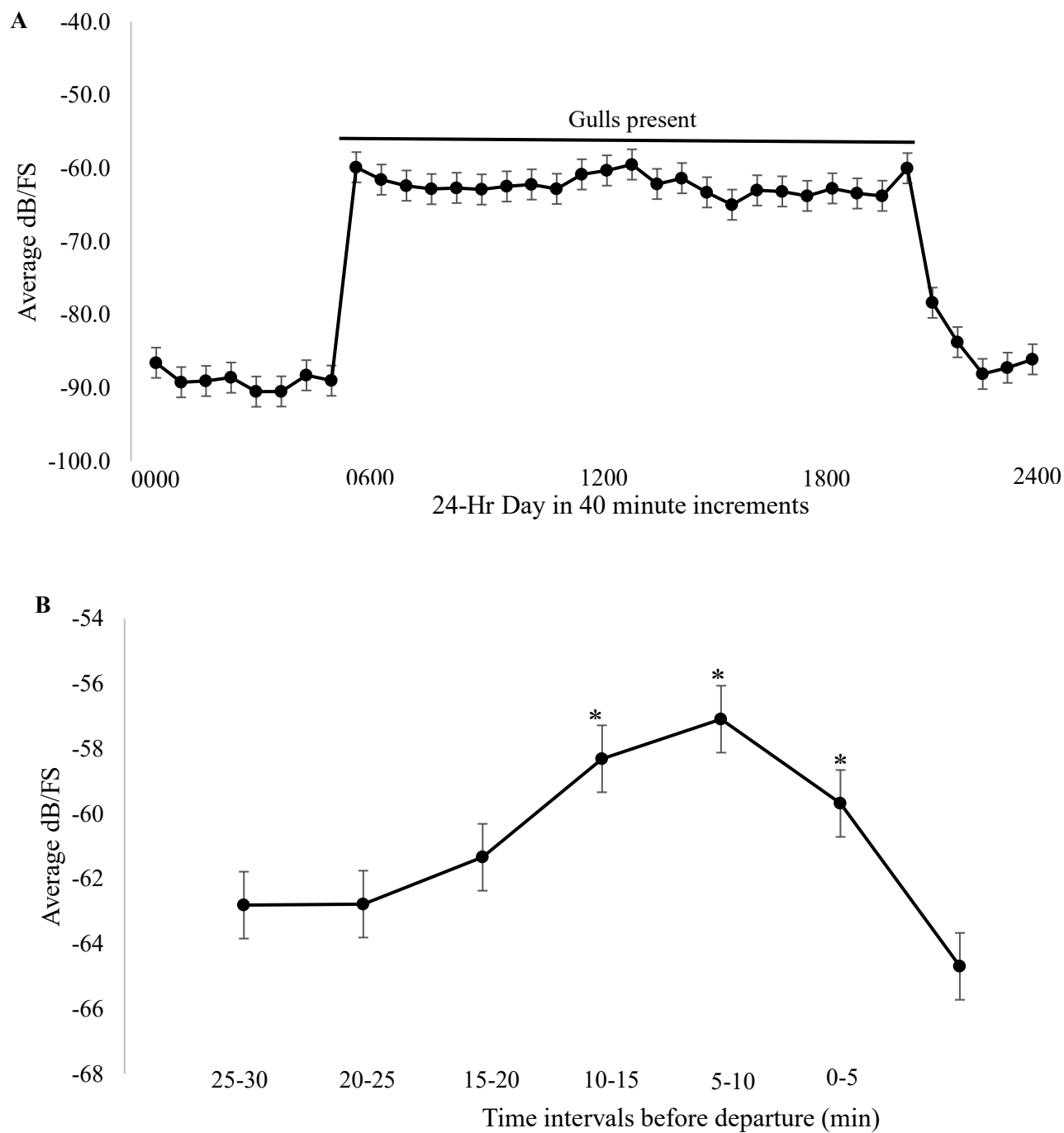
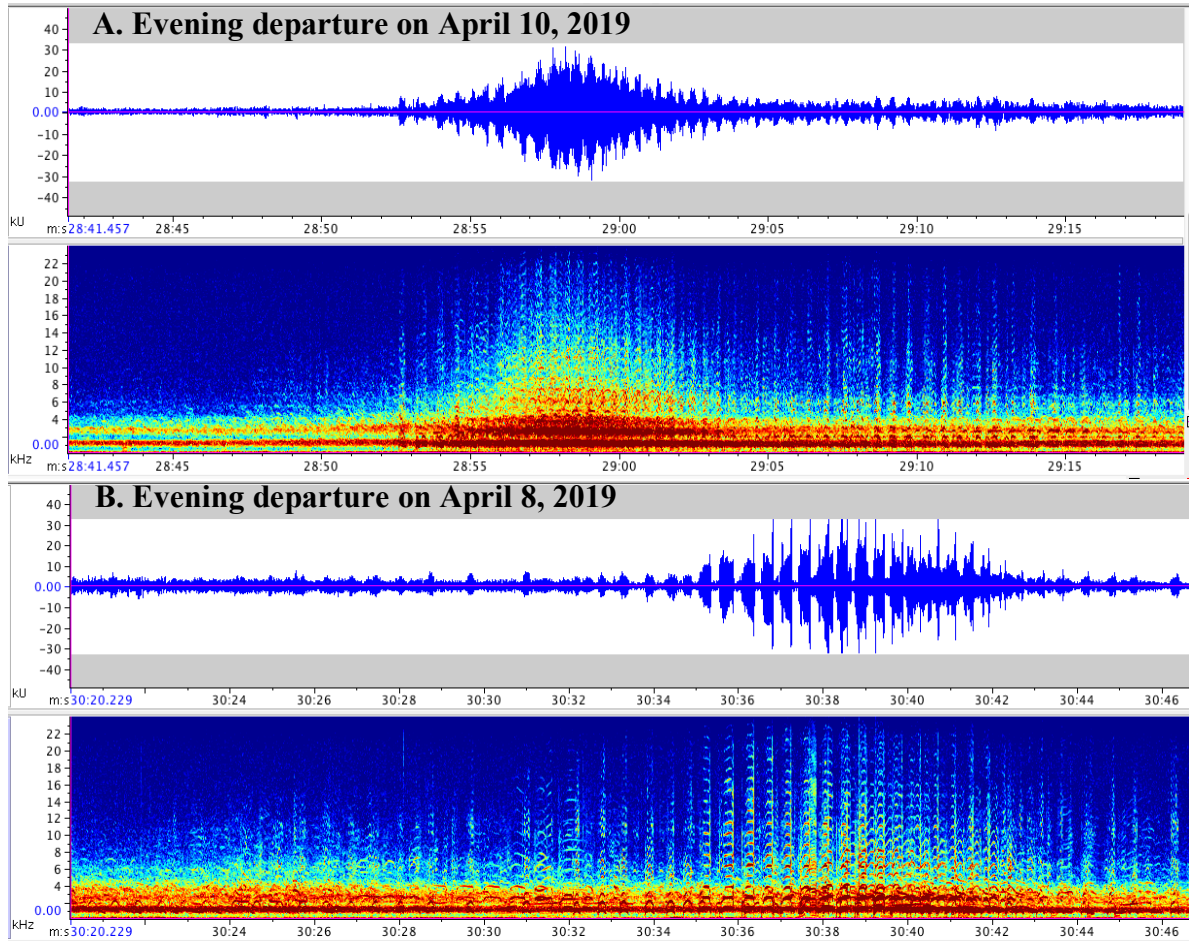


Figure 4. The average sound intensity for acoustic recordings. The average sound intensity for 7 days recorded at two locations for (A) 24-hour period in 40-minute increments and (B) for 30 min prior to nighttime departures in 5-min intervals. Error bars represent standard error. Asterisks denote intervals that were determined to be significant. Error bars represent standard error.



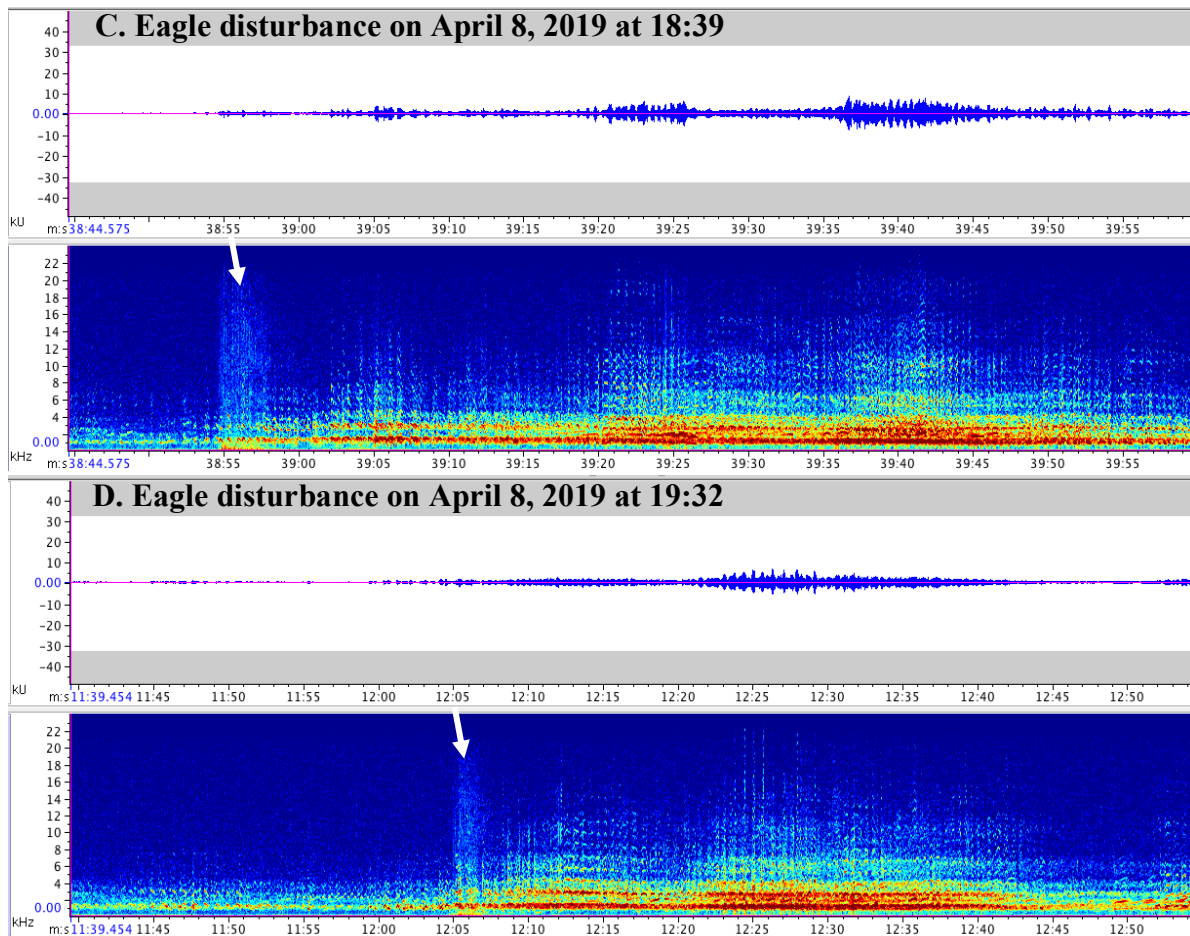


Figure 5. Representative sonograms and spectrograms of acoustic recordings. The representative sonograms and spectrograms of (A,B) evening departures and (C,D) eagle disturbances recorded by the *Swift* units. The representative departures were recorded on the evenings of (A) April 10 and (B) April 8, 2019 while the eagle disturbances were recorded on April 8, 2019 at (C) 18:39 and (D) 19:32. The acoustic signature of the eagle disturbance is indicated by the white arrows. The gull calls are indicated within the white brackets. Gulls calls after the eagle disturbance were variable (white brackets).

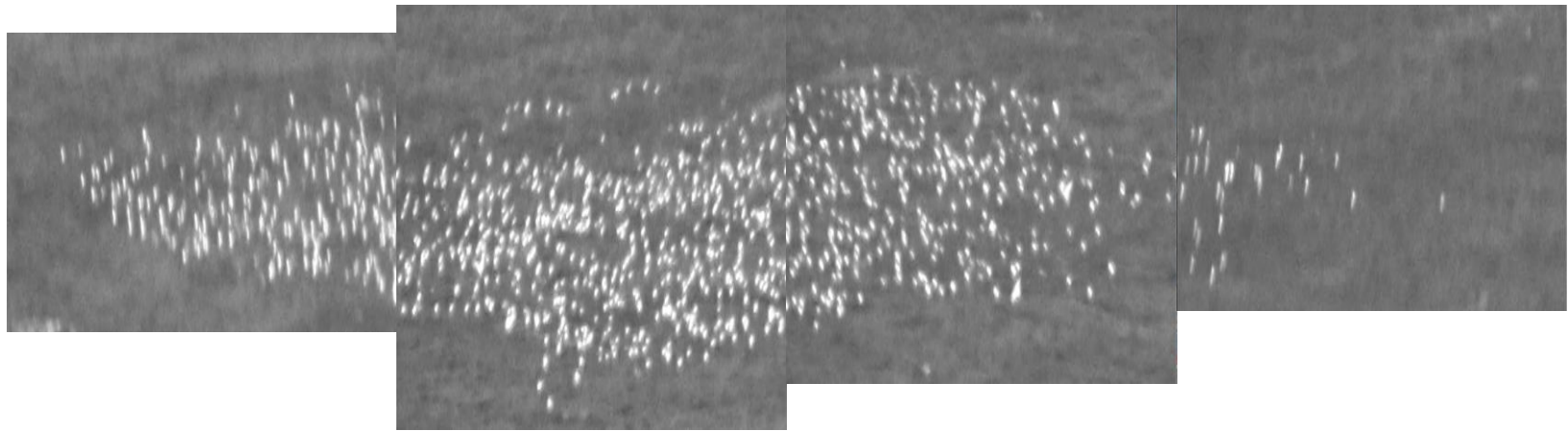


Figure 6. Composite infrared image of the northern raft. Composite infrared image of the northern raft taken on May 17, 2016 at 21:22.

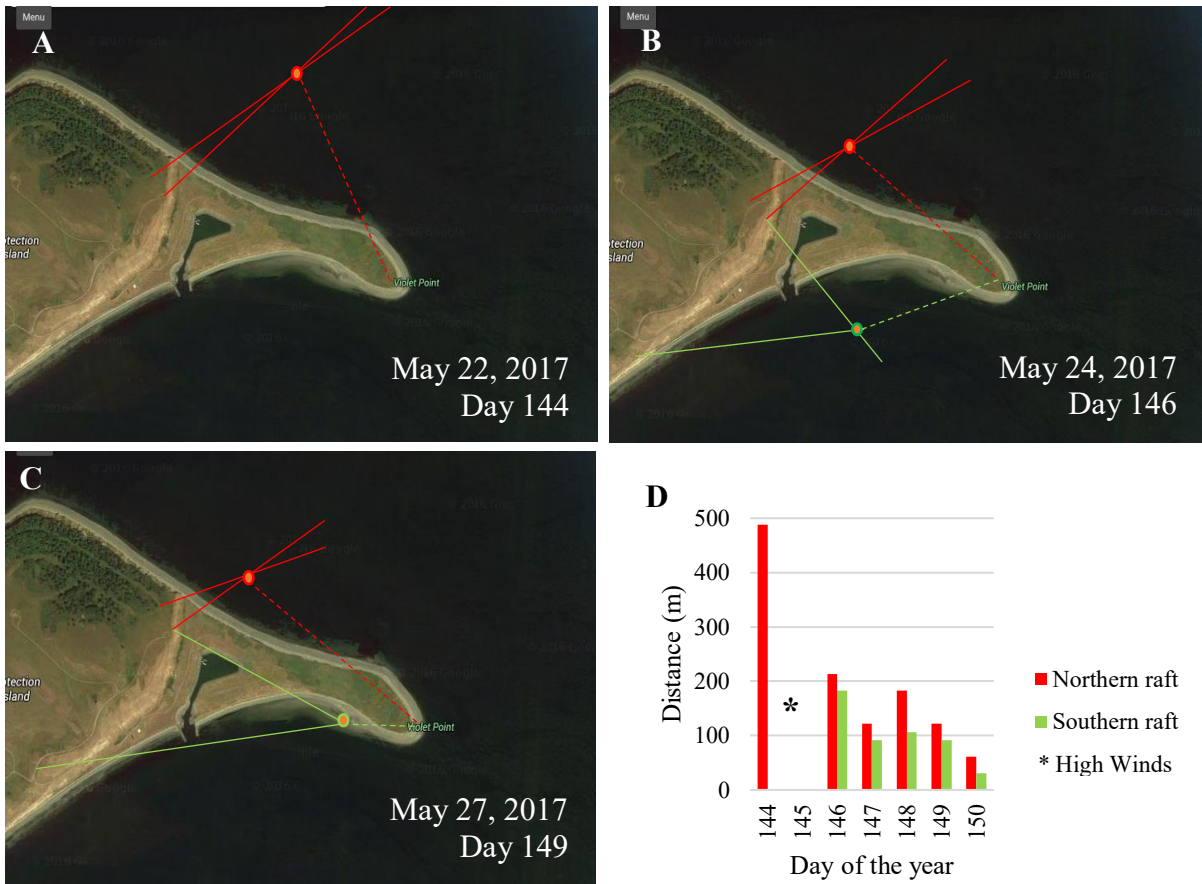


Figure 7. The estimated locations of rafts. The estimated locations of the rafts of gulls to the north and south of Violet Point based on triangulation data (A-C). The dotted lines represent the distance from the fixed reference of Violet Point. The bar graph (B) shows the distance of the rafts to Violet Spit as the season progresses. On day 144, the southern raft was too far away from the island to triangulate. On Day 143, the southern raft was too far from the island to triangulate the location of the raft.

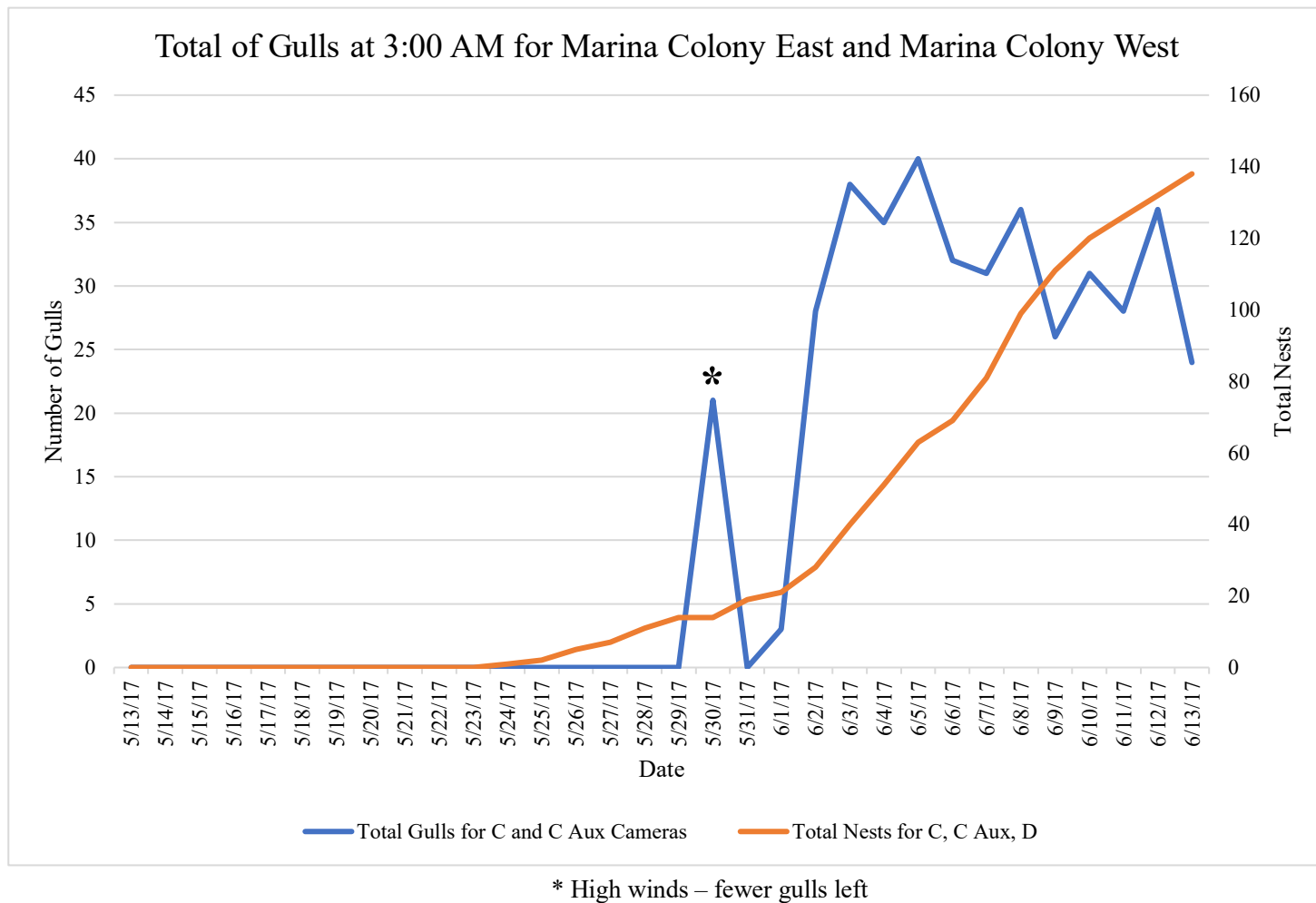


Figure 8. The total number of gulls present against the number of clutches initiated. The total number of gulls present on both Marina Colony East and Marina Colony West at 3 AM from mid-May to mid-June in 2017 plotted against the number of clutches initiated on the corresponding days.

