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Avian Behavior, Ecology, and Evolution

Patterns of inter- and intraspecific nest dispersion in colonies of gulls and grebes based on drone imagery

Patrones de dispersión de nidos inter e intraespecíficos en colonias de gaviotas y zambullidores basados en imágenes de drones

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ABSTRACT. Colonial nesting of both single and mixed-species assemblages is common across avian taxa. Coloniality may provide fitness advantages such as reduced nest predation through predator swamping, early warning of predators, or nest stability, or could simply arise through individuals selecting similar high-quality habitats. Traditionally, studies of nest dispersion in marsh-nesting colonial birds have required the use of on-the-ground methods due to the difficulty of accessing nesting areas and the cryptic nature of nests. Here, I make use of drone-borne thermal and visible sensors to capture imagery of a large sample of nests (~1,700) at single and mixed-species colonies of two grebe species and one gull species nesting at four marshes in Saskatchewan, Canada. As predicted, species exhibited significant intraspecific nest clustering, with individuals nesting closer together than expected by chance more often than not (in nine of 13 species-subcolony comparisons, where subcolonies were delineated based on aggregations of nests within marshes). In contrast, grebe species rarely nested closer to Franklin's Gulls (*Leucophaeus pipixcan*) than expected by chance, contrary to theoretical predictions based on presumed advantages of anti-predator defense or nest stability from gulls. As predicted, the larger (Western Grebe, *Aechmophorus occidentalis*) and more aggressive species (Franklin's Gull) had greater nearest neighbor distances than the smallest species (Eared Grebe, *Podiceps nigricollis*). Nearest neighbor distances tended to be smaller at subcolonies with greater emergent vegetation cover and at larger subcolonies, which may be due to reduced visibility allowing for smaller distances between neighbors, and social attraction at larger subcolonies, respectively. While valuable from a population monitoring perspective, this study demonstrates that high-resolution imagery from drones can also aid in answering ecological questions, and in combination with detailed nest success information, could help identify habitat needs and potential factors limiting reproductive success of declining and sensitive marsh species.

RESUME_. La anidación colonial de conjuntos de especies individuales y mixtas es común entre los taxones de aves. La colonialidad puede proporcionar ventajas de aptitud, como la reducción de la depredación de los nidos a través de la sobre oferta a los depredadores, la advertencia temprana de depredadores, la estabilidad de los nidos, o simplemente podría surgir a través de los individuos la selección de hábitats similares de alta calidad. Tradicionalmente, los estudios sobre la dispersión de nidos en aves coloniales que anidan en las marismas han requerido el uso de métodos sobre el terreno debido a la dificultad de acceder a las áreas de nidificación y a la naturaleza críptica de los nidos. En este caso, utilicé sensores térmicos y visibles a bordo de drones para capturar imágenes de una gran muestra de nidos (~1.700) en colonias compuestas por una y varias especies, utilizando los nidos de dos especies de zambullidores y una especie de gaviota que anidan en cuatro marismas de Saskatchewan, Canadá. Tal y como se preveía, las especies mostraron una importante agrupación de nidos intraespecíficos, con individuos que anidaban con más frecuencia más cerca que de lo esperado por el azar (en nueve de las 13 comparaciones entre especies y subcolonias, en las que las subcolonias se delimitaron basándose en agregaciones de nidos dentro de los pantanos). Por el contrario, las especies de zambullidores rara vez anidaron más cerca de las gaviotas de Franklin (Leucophaeus pipixcan) de lo que se esperaba por azar, en contra de las predicciones teóricas basadas en las supuestas ventajas de la defensa contra los depredadores o la estabilidad de los nidos de las gaviotas. Como se preveía, las especies más grandes (zambullidor occidental, Aechmophorus occidentalis) y más agresivas (gaviota de Franklin) tenían mayores distancias entre vecinos más cercanos que la especie más pequeña (zambullidor orejudo, Podiceps nigricollis). Las distancias entre vecinos más cercanos tienden a ser menores en las subcolonias con mayor cobertura de vegetación emergente y en las subcolonias más grandes, lo que puede deberse a una menor visibilidad que permite menores distancias entre vecinos y a la atracción social en las subcolonias más grandes, respectivamente. Además de ser valioso desde el punto de vista del seguimiento de la población, este estudio demuestra que las imágenes de alta resolución obtenidas con drones también pueden ayudar a responder a cuestiones ecológicas y, en combinación con información detallada sobre el éxito de los nidos, podrían ayudar a identificar las necesidades de hábitat y los posibles factores que limitan el éxito reproductivo de las especies de marismas que están en declive y son sensibles.

Key Words: *drone; colony; marsh bird; nearest neighbor; nest; Unoccupied Aerial Vehicle; waterbird*

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INTRODUCTION

Colonial nesting is present across most avian groups and is estimated to occur in anywhere from 13-30% of species (Lack 1968, Crook 1965, Rolland et al. 1998). Variability in this estimate is likely due to differences in how a colony is defined and because many species exist on a gradient between solitary and colonial breeding (Brown and Brown 2001); regardless, colonial breeding can generally be defined as conspecific breeding among densely distributed territories that contain no resources other than a nest (Danchin and Wagner 1997). The prevalence of colonial breeding among avian species has been associated with the absence of a feeding territory, a preference for aquatic habitats, and the degree of nest exposure to predators, with coloniality being especially prominent in waterbirds and seabirds (Rolland et al. 1998). Colonial breeding is considered somewhat of an evolutionary puzzle because individuals pay fitness costs from nesting at high densities, for example from intraspecific competition and increased parasite loads (Brown and Brown 1996), but several adaptive benefits have also been proposed, mostly centered around reduced predation risk and enhanced foraging efficiency (Picman et al. 1988, Danchin and Wagner 1997). Alternatively, the commodity selection theory posits that coloniality arises as a byproduct of individuals selecting habitats or mates and does not necessarily provide fitness advantages (Wagner et al. 2000).

Although most prevalent among seabirds, many North American species of inland waterbirds exhibit colonial breeding, including several species of marsh-nesting gulls, grebes, terns, and herons. Previous work on marsh-nesting colonial birds demonstrated both advantages and disadvantages associated with colonial nesting. Eared Grebes (*Podiceps nigricollis*) nesting in colonies with smaller neighbor distances suffered greater intraspecific brood parasitism, egg loss, and infanticide, but less predation by American Coots (*Fulica americana*) (Hill et al. 1997), while the prevalence of coloniality in Red-necked Grebes (*P. grisegena*) was linked to high-quality habitats but colonial breeding itself did not provide direct fitness benefits (Sachs et al. 2007). Studies of Franklin's Gulls (*Leucophaeus pipixcan*) showed that nest dispersion was related to vegetation thickness, with smaller neighbor distances occurring in areas with thicker vegetation, presumably due to a decline in visibility resulting in reduced aggression towards neighbors (Burger 1974a). Thus, there are likely species-specific trade-offs that relate to both the presence and degree (e.g., nest dispersion distances, colony size, etc.) of coloniality.

In addition to single-species colonies, many colonial breeders form mixed-species colonies, which may have their own trade-offs. Nesting in mixed-species colonies may allow for some of the advantages of coloniality, but with less intraspecific competition (Krebs 1974, Burger 1981). On the other hand, other species may act as predators or more efficient competitors (Burger and Shisler 1978, Ellis and Good 2006). Some species may gain advantages from alarm calls and anti-predator behavior or habitat modifications of heterospecific colony members. For example, Western Grebes (*Aechmophorus occidentalis*) have been shown to respond to Forster's Tern (*Sterna forsteri*) alarm calls in mixed-species colonies by covering their eggs with vegetation and quickly leaving their nest (Nuechterlein 1981), and both Silvery (*P. occipitalis*) and Rolland's grebes (*Rollandia rolland*) respond to the alarm calls of Brown-hooded Gulls (*Chroicocephalus maculipennis*) and have higher reproductive success when nesting in association with the gulls (Burger 1984). Eared Grebes are commonly found in association with Larids worldwide (Nuechterlein 1981), and in North America appear to benefit from greater nest stability by anchoring their nests to those of Franklin's Gulls (Burger and Gochfeld 1995).

Studies of nest dispersion in marsh-nesting colonial birds have traditionally been conducted using on-the-ground methods (e.g., via wading or small boat) (Burger 1974a, Hill et al. 1997, Trimble and Green 2018). As a result, often only a subsample of nests from an entire colony are surveyed and sample sizes may be small, while the level of disturbance to individuals and marsh vegetation is high, and the time and effort required to conduct the survey is extensive. Unoccupied Aerial Vehicles, or drones, represent a new tool for studying and monitoring population abundance of these species and their nests (Lachman et al. 2020, McKellar et al. 2021). Although drones may not be able to capture as detailed reproductive success data as can ground-based methods (Callaghan et al. 2018), they may be able to provide large sample sizes of nests from multiple colonies for studies of the correlates of inter- and intraspecific nest dispersion with less disturbance.

In this study, I used drone-borne thermal and visible sensors to capture imagery of a large number of nests (~1,700) at single and mixed-species colonies of one gull species (Franklin's Gull) and two grebe species (Western and Eared grebes) to test predictions related to nest dispersion. I first examined intraspecific nest clustering, and I predicted that nests would be clustered together more than expected by chance based on the theoretical advantages of coloniality. I then asked whether, in mixed-species colonies, grebe nests clustered with gull nests. I predicted that grebes would nest closer to gulls than expected by chance due to expected advantages received through predator warning and/or nest stability. Finally, I asked whether intraspecific nearest neighbor distance varied by species and colony characteristics (vegetation density and colony size). I predicted that Franklin's Gulls, the most aggressive of the three species, and Western Grebes, the largest species, would have greater nearest neighbor distances than the less aggressive and smallest Eared Grebe. I predicted that colonies with greater vegetation density and those that are larger (i.e., greater number of nests) would be associated with smaller nearest neighbor distances.

METHODS

Study species

Franklin's Gulls, Western Grebes, and Eared Grebes generally nest colonially within interior North America in shallow freshwater marshes with sufficient open water and emergent vegetation within which nests are built, often forming mixed-species colonies with each other as well as with other waterbirds such as Black Terns (*Chlidonias niger*), Forster's Terns, and Black-crowned Night Herons (*Nycticorax nycticorax*) (Burger and Gochfeld 2020, Cullen et al. 2020, LaPorte et al. 2020). Colonies may be ephemeral and shift from year to year based on changes in water levels and vegetation structure; all three species are vulnerable to human disturbance and are known to desert colonies if disturbed early in their breeding cycle. Western and Eared grebes rarely fly except during migration. When disturbed by mammalian predators, including humans, they will often attempt to cover eggs with vegetation and retreat by diving or swimming on the surface to open water, leaving eggs exposed to predators (Cullen et al. 2020, LaPorte et al. 2020). Franklin's Gulls are a more aggressive species and are known to respond to predators via swoop-and-soar flights, mobbing, and attacking (Burger and Gochfeld 2020). Although quality long-term monitoring data from breeding populations are generally lacking for these species and thus population trends are uncertain, Western Grebes have been listed federally in Canada as a species of Special Concern due to perceived declines on the wintering grounds (COSEWIC 2014).

The Western Grebe is the largest of the three species (55-75 cm long; 800-1800 g), with nest platforms that range from ~50 cm to 1.2 m in diameter and are ~9-15 cm above water (LaPorte et al. 2020). Nests typically occur in flooded emergent vegetation, built up from the bottom of the lake or anchored to emergent or floating plants, in which adults pile material from the lake bottom. The degree of coloniality is highly variable, ranging from pairs nesting singly or in small groups, to colonies of up to several thousand birds. Reported nearest neighbor distances are typically 2-3.9 m and tend to be larger when water levels are higher (LaPorte et al. 2020). Franklin's Gulls are smaller (32-36 cm long; 250-325 g) with a similar range of nest diameters to the Western Grebe (~58 cm - 1 m) that are generally higher above the water (14-40 cm). Nesting occurs in sparse stands of emerging vegetation, or sometimes in moderately dense cattails, with preferred sites having a mat of vegetation at the surface that is anchored to rooted vegetation. Once construction is complete, nests will sink over time and adults must add new material throughout incubation and brooding, which is often stolen from neighboring gulls. A highly gregarious species, colonies consist of hundreds up to > 100,000 pairs (Burger and Gochfeld 2020). During incubation, nearest neighbor distances are typically 2-3 m (Burger 1974a). Finally, the Eared Grebe is similarly sized to the Franklin's Gull (28-35 cm long; mass highly variable depending on season, but averages 325 g during breeding), with small, highly cryptic nests that are 20-34 cm in diameter and 8-15 cm above water. Nests are usually placed on a foundation of bent-over reeds which the birds cover with plant matter from the lake bottom and anchor to emergent or submergent vegetation, or floating algae (Cullen et al. 2020). Small groups and solitary pairs may nest in smaller marshes, but typically dense nesting colonies of hundreds of pairs are found in larger marshes, with reported nearest neighbor distances of 0.5-3 m (Hill et al. 1997).

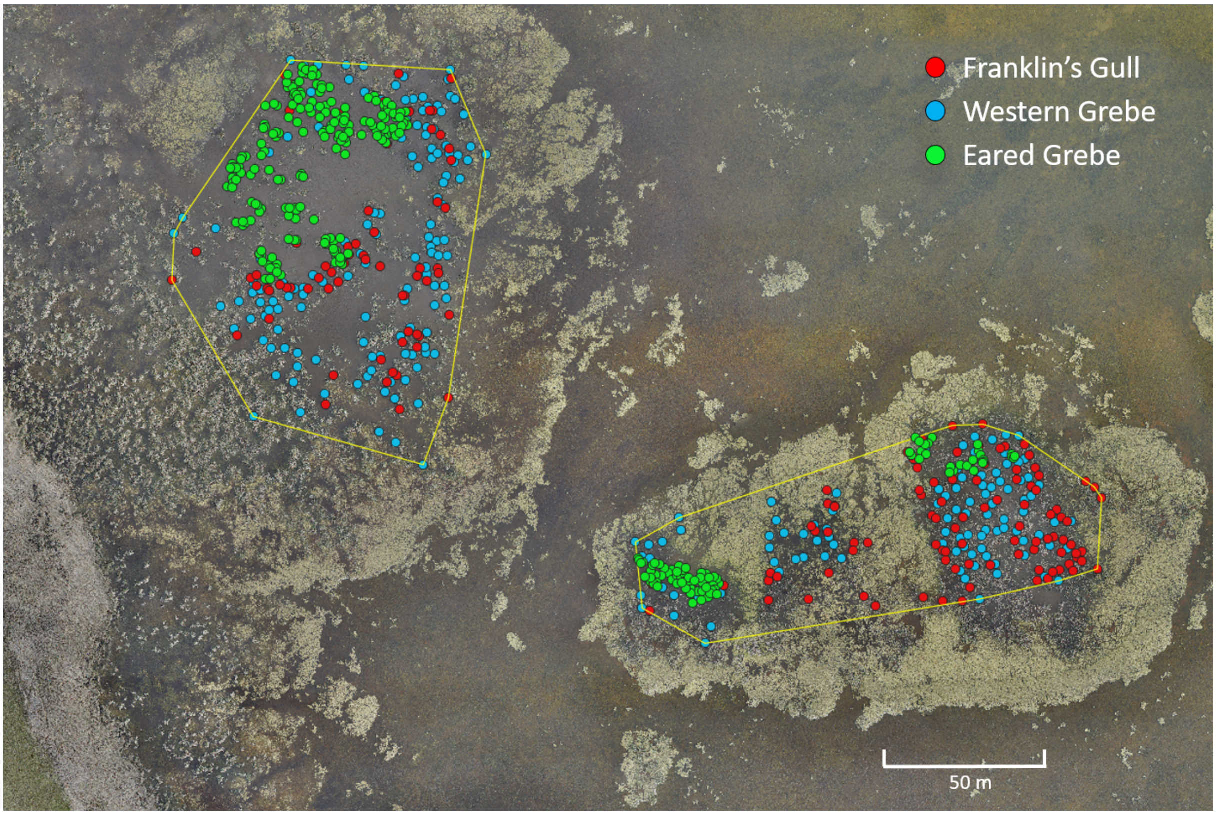
Drone surveys and data processing

Drone surveys were conducted at four marshes in Saskatchewan, Canada, in June 2018 and 2019 (Table 1). Work conducted in 2019 is described in detail in McKellar et al. (2021). In brief, marshes were visited in May and June to confirm nesting of the focal species, which included Western Grebe, Franklin's Gull, Black Tern, Forster's Tern, and Black-crowned Night-Heron (in McKellar et al. 2021). Prior to drone surveys, each marsh was surveyed on the ground (by wading or kayaking), in mid-June to coincide with the mid-incubation period, to obtain nest counts for each species to compare to the drone-based nest counts. Ground surveys were conducted by two observers who traversed each colony in parallel transects spaced 4 m apart and recorded all nests within 2 m on either side of the transect, until the entire colony was surveyed. Drone surveys were then conducted within seven days of ground surveys at each marsh, covering the same areas as the ground surveys, using a ~9-kg octocopter based on the DJI S1000+ airframe (SZ DJI Technology Co. Ltd., Shenzhen, Guangdong, China) and Pixhawk2 flight controller (Hex Technology Ltd., Sha Tin, Hong Kong) carrying both a visible (Sony α7R, 36-megapixel resolution and 28-mm lens, Sony Corporation, Minato, Tokyo, Japan) and a thermal-infrared camera (FLIR Vue Pro R, 640 x 512-pixel resolution and 13-mm lens, FLIR Systems, Wilsonville, Oregon, USA). Images were post-processed into orthomosaics using OneButton Standard 5.1 (Icaros, Manassas, Virginia, USA). Using QGIS 3.2 (QGIS Development Team 2018), nests of focal species were annotated and counted in separate point shapefiles. Based on differences in the size and structure of each of the focal species' nests, and the high-resolution visible imagery (0.8-1 cm/pixel), nests could confidently be assigned to species by an experienced observer (McKellar et al. 2021). For the current study, I added counts of Eared Grebes at two marshes where they occurred. Counts were made using the visible imagery, while also checking the thermal-infrared imagery to confirm what was suspected to be a nest as well as to detect and confirm the location of nests that were not immediately seen in the visible imagery. In all cases, drone-based counts were within a 5% difference from ground-based counts for Western Grebes and Franklin's Gulls; a similar comparison for Eared Grebes is not possible because ground-based counts were not conducted by McKellar et al. (2021). In addition, McKellar et al. (2021) did not detect any visible disturbance to bird behavior by the drone at the altitudes flown.

I added one additional marsh based on work conducted in 2018 that used similar methods. The only differences during the 2018 survey were that a smaller quadcopter was used (Phantom 4, DJI, Shenzhen, China) and only visible imagery was captured, using the drone's on-board camera (12.4 megapixel resolution and a 20-mm lens). Ground-based survey methodology was identical and showed that drone-based nest counts for Franklin's Gulls (the only species nesting at that marsh) were < 1.5% different from ground-based counts.

Due to the clumped nature of individual nests within marshes, I created a set of rules to define and delineate separate "subcolonies" at each marsh. This approach allowed for the exclusion of unsuitable nesting habitat between clumps of nests, which otherwise would have biased results in the nearest neighbor analysis towards a greater likelihood of significance (i.e., smaller distances observed than expected by chance, due to no nests in unsuitable habitat). A subcolony was defined as an area where nesting occurred by at least one focal species at a marsh in which there was never an open-water gap of > 15 m between nests of focal species. These subcolonies appeared to coincide with "natural" breaks in the marshes, based on visual examination of the imagery (Fig. 1), as well as personal observation on the ground - e.g., birds from within a subcolony tended to flush during a ground survey, while those from a separate subcolony would not. Therefore, this allowed for the exclusion of open-water areas or solid ground, while still providing a reasonable number of sampling units as random effects with sufficient sample of nests within each unit. In total, there were seven subcolonies present in the four marshes (Table 1).

Fig. 1. Sample drone imagery at two mixed-species subcolonies of Franklin's Gulls (*Leucophaeus pipixcan*), Western Grebes (*Aechmophorus occidentalis*), and Eared Grebes (*Podiceps nigricollis*). Minimum convex hulls show the delineation of the two subcolonies.



To quantify vegetation density at each subcolony, I calculated a mean percentage of emergent vegetation based on randomly selected points within each subcolony. This was done in QGIS by first creating a minimum convex hull around all nests within a subcolony, then generating 30 random points within the hull, and finally creating a 1 m radius buffer around each point. I then visually assessed the percentage of emergent vegetation within each buffer.

Data analysis

Intraspecific nearest neighbor distance

I conducted nearest neighbor (NN) analysis for each species at each subcolony using the Nearest Neighbor Analysis tool in QGIS. With individual nests as the sampling unit, this algorithm calculates the observed mean NN distance for each nest ($\langle D_O \rangle$), and an expected mean NN distance, given as:

$$\langle D_E \rangle = \frac{0.5}{\sqrt{n / A}} \tag{1}$$

where n is the total number of species-specific nests and A is the area of a minimum bounding rectangle surrounding the nests of each species. A z-score is then calculated as:

$$z = \frac{\langle D_0 \rangle - \langle D_E \rangle}{SE} \tag{2}$$

where

$$SE = \frac{0.26136}{\sqrt{n^2 / A}} \tag{3}$$

Due to multiple comparisons, I used Bonferroni correction when interpreting p-values at each subcolony. With 13 total tests, I considered a NN distance to be significant (i.e., smaller than expected by chance) at an alpha level of 0.0038. I also conducted a paired t-test to evaluate whether observed and expected NN distances differed from each other across all subcolonies, with each subcolony-by-species combination as the sampling unit. This test allowed for an examination of overall nest dispersion patterns across the species and subcolonies surveyed, although it did not discriminate species or subcolony-specific differences as in the above analysis.

Interspecific nest dispersion

To test whether grebes nested closer to gulls than expected by chance, I conducted a similar analysis to the NN analysis, but it was done in several steps as there is no automated tool to do this comparison between points from different shapefiles in QGIS. I first used the Distance Matrix tool in QGIS to calculate the distance between each species of grebe's nest and the nearest gull nest at each subcolony. From this, I calculated the observed mean distance ($\langle D_O \rangle$), and I took the expected mean distance ($\langle D_E \rangle$)

Table 1. Marshes and their associated subcolonies where nests of one or more focal species of grebe or gull was counted via drone imagery. Number of nests of each species, percent emergent vegetation, and mean nearest neighbor distances (m) with SD in brackets for each species is shown for each subcolony. P-values indicate whether intraspecific nearest neighbor distances were significantly closer than expected by chance, at an alpha level of 0.0038 due to Bonferroni correction (see text). Significant values are noted by an asterisk.

Marsh	Subcolony	Species	# nests	% vegetation	NN (SD)	P-value
Jackfish Lake	A	Franklin's Gull	72	30	4.32 (3.4)	0.0014*
Jackfish Lake	B	Franklin's Gull	96	34.5	3.57 (2)	0.0004*
Foam Lake	C	Franklin's Gull	201	52.5	1.12 (0.54)	<0.0001*
Foam Lake	D	Franklin's Gull	236	42	1.17 (0.74)	<0.0001*
Hazel Lake	E	Franklin's Gull	174	56.5	1.59 (0.9)	<0.0001*
Hazel Lake	F	Franklin's Gull	63	78	1.34 (0.49)	0.0444
Jackfish Lake	A	Western Grebe	139	30	3.73 (1.99)	0.0002*
Jackfish Lake	B	Western Grebe	102	34.5	3.62 (1.26)	0.0004*
Quill Lake	G	Western Grebe	40	17	5.74 (2.73)	0.4867
Jackfish Lake	A	Eared Grebe	196	30	1.25 (0.68)	<0.0001*
Jackfish Lake	B	Eared Grebe	92	34.5	1.19 (0.52)	<0.0001*
Foam Lake	C	Eared Grebe	153	52.5	0.9 (0.32)	0.1293
Foam Lake	D	Eared Grebe	129	42	0.99 (0.43)	0.0108

and number of nests (n) from the output provided in the NN analysis above. Finally, I used the Minimum Bounding Geometry tool to obtain a minimum bounding rectangle surrounding the grebe nests (A) and calculated a z-score using the above formulas. With six total tests, I considered the interspecific nest distance to be significant at an alpha level of 0.0083. As above, I also conducted a paired t-test of observed versus expected nest distances across the six subcolonies.

Correlates of intraspecific nearest neighbor distance

I examined the influence of species and subcolony characteristics on NN distance using a generalized linear mixed model (GLMM) with a Gamma distribution and log link. This distribution is appropriate for positive, continuous response variables that do not include zero (Zuur et al. 2009). Predictor variables included species, vegetation density, and species-specific subcolony size (i.e., number of nests of that species at the subcolony); subcolony ID was included as a random effect. No variables were correlated (all r < 0.3). I chose to not include any interactions in order to keep the interpretation of results simple, and because preliminary data exploration did not reveal any potential strong interactions. I validated models by examining plots of residuals versus fitted values and versus each covariate and did not detect any non-linear or other patterns. I tested the significance of each predictor using the likelihood ratio test in the 'drop1' function ('stats' package, R Core Team 2020), which compares the full and reduced models by dropping a single predictor at a time. Unless otherwise noted, I considered variables significant at an alpha level of 0.05. All analyses were conducted in R v. 4.0.3 (R Core Team 2020).

RESULTS

There were a total of 1,693 nests at the seven subcolonies, with Franklin's Gulls being the most numerous species (N = 842 nests) and occurring at six subcolonies, followed by Eared Grebes (N = 570 nests), which occurred at four subcolonies, and Western Grebes (N = 281 nests), which occurred at three subcolonies (Table 1). Percent vegetation at the subcolonies ranged from 30-78% (mean = 44%), and species-specific number of nests ranged from 40-236 (mean = 130; Table 1).

Inter- and intraspecific nest dispersion

Franklin's Gull nests exhibited significant clustering at five of six subcolonies. Western and Eared grebe nests exhibited significant clustering at two of three, and two of four subcolonies, respectively (Table 1). Overall, NN distances were smaller than expected by chance across all subcolony-by-species combinations (t = -3.08, P = 0.0095).

Western Grebe nests were randomly distributed in relation to Franklin's Gull nests, whereas Eared Grebes nested closer to gulls than expected by chance at two of four subcolonies, further than expected at one subcolony, and were randomly distributed at one subcolony (Table 2). Across all subcolony-by-species combinations, interspecific nest distances did not differ than expected by chance (t = 0.733, P = 0.496).

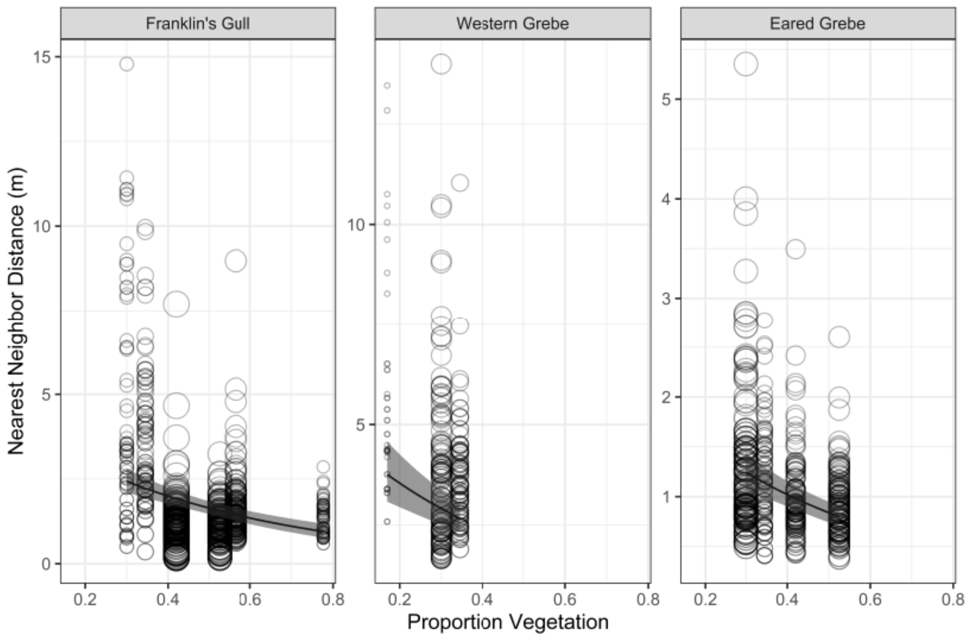
Table 2. Interspecific nest dispersion between each grebe species and nearest Franklin's Gull nest, at each of four subcolonies and two marshes where co-nesting between grebes and gulls occurred. Mean distance (m) between grebe and the nearest gull nest is shown, with SD in brackets. P-values indicate whether intraspecific nest distances were significantly closer than expected by chance, at an alpha level of 0.0083 due to Bonferroni correction (see text). Significant values are noted by an asterisk, and symbols indicate whether distances are significantly greater (+) or smaller (-) than expected by chance.

Marsh	Subcolony	Species	Nest dispersion	P-value
Jackfish Lake	A	Western Grebe	4.94 (3.78)	0.0183
Jackfish Lake	B	Western Grebe	4.2 (3.33)	0.3163
Jackfish Lake	A	Eared Grebe	6.22 (5.78)	<0.0001* (+)
Jackfish Lake	B	Eared Grebe	3.12 (1.86)	0.0004* (-)
Foam Lake	C	Eared Grebe	0.87 (0.308)	0.031
Foam Lake	D	Eared Grebe	0.82 (0.273)	<0.0001* (-)

Correlates of intraspecific nearest neighbor distance

Nearest neighbor distances varied significantly by species (χ^2 = 584.1, P < 0.001). Distances were greatest in Western Grebe (3.98

Fig. 2. Relationship between proportion vegetation at a subcolony and nearest neighbor distance for Franklin's Gulls (*Leucophaeus pipixcan*), Western Grebes (*Aechmophorus occidentalis*), and Eared Grebes (*Podiceps nigricollis*), with subcolony included as a random effect. Circle size is proportional to subcolony size (species-specific number of nests at the subcolony).



± 2.02 m), followed by Franklin's Gull (1.8 ± 1.73 m) and Eared Grebe (1.09 ± 0.54 m). Subcolonies with greater vegetation density (χ^2 = 12.81, P < 0.001) and those that were larger (χ^2 = 204.5, P < 0.001) exhibited smaller NN distances (Fig. 2).

DISCUSSION

Most previous work on nest placement in marsh birds has relied on ground-based methods, which can be highly disruptive to nesting birds and their habitats, time-consuming, and often result in limited sample sizes. Here, I studied the spatial distribution of nests of three species of marsh-nesting colonial grebes and gulls using a large dataset of ~1,700 nests obtained from drone aerial imagery. Previous work demonstrated that such aerial counts were highly congruent with ground-based counts that used much more intensive methods while causing minimal disturbance to birds (McKellar et al. 2021). While clearly valuable from a population monitoring perspective, the current study demonstrates that high-resolution imagery from drones can also help to answer ecological questions. As predicted, species exhibited significant intraspecific nest clustering, with individuals nesting closer together than expected by chance more often than not (in nine of 13 species-subcolony comparisons). In contrast, grebe species nested closer to Franklin's Gulls than expected in only two of six comparisons, contrary to my prediction which was based on presumed advantages of anti-predator defense or nest stability from gulls. As predicted, the larger (Western Grebe) and more aggressive species (Franklin's Gull) had greater nearest neighbor distances than the smallest species (Eared Grebe), and nearest neighbor distances tended to be smaller at subcolonies with greater emergent vegetation cover and at subcolonies that were larger (i.e., more conspecific nests).

While Eared Grebes had the smallest neighbor distances, significant clustering of intraspecific nests was seen more often in Franklin's Gulls than in the two grebe species. Nonetheless, Western and Eared grebes each exhibited significant clustering in at least half of the subcolonies where they occurred. Franklin's Gulls are a highly gregarious and social species, exhibiting extensive courtship displays on nest platforms prior to incubation, frequent stealing of nest material among neighbors during incubation, and joint mobbing of aerial and mammalian predators (Burger 1974a, Burger and Gochfeld 2020), which may explain the greater nearest neighbor distances, but also significant clustering, compared to the similarly sized but less aggressive Eared Grebe. Benefits of nesting closer to conspecifics could include the synchronization of egg-laying, enhanced predator detection, and reduced predation risk through predator swamping (Descamps 2019). In the Eared Grebe, Hill et al. (1997) showed that there was greater intraspecific aggression, brood parasitism, and egg loss, but lower predation from American Coots, when nests were placed closer together; thus, the benefits of nesting closer to conspecifics in the Eared Grebe could depend on colony-specific predation risk. Alternatively, patterns of nest dispersion in the three species could be influenced by habitat structure (Wagner et al. 2000). While I was able to eliminate most larger areas of unsuitable habitat (e.g., open water) when delineating subcolonies, emergent vegetation may still be patchily distributed within subcolonies, and individuals could respond similarly to patterns of vegetation structure when deciding where to nest, rather than to the presence of conspecifics per se. Previous work has shown that Franklin's Gulls prefer to nest in cattail stands next to open water and will avoid areas where cattail density is too great (Burger 1974a). In the Western Grebe, nests located near the open-water colony edge tend to be less successful than those in the interior, due to the negative impact of storms and wave activity on exposed nests (Allen et al. 2008); furthermore, the degree of nest clustering has previously been related to annual variation in water levels (LaPorte et al. 2020). I found a similar result, in that the one Western Grebe subcolony with the lowest percent emergent vegetation (i.e., most open water) also showed non-significant nest clustering and the largest mean nearest neighbor distance (subcolony G, Table 1). Nonetheless, the birds themselves have the ability to modify the habitat to some degree - especially the grebe species, which may build their nests up from the lake bottom or use floating vegetation - which may negate some of the effects of vegetation patchiness on nest dispersion.

Many bird species appear to benefit from nesting in association with more aggressive 'protector' species, which may result in reduced nest predation and early warning of predators (Quinn and Ueta 2008). Eared Grebes are the most abundant grebe worldwide and frequently nest in mixed-species colonies across their range in North America and Eurasia (Bochenski 1961, Cullen et al. 2020). In addition to anti-predator protection, previous work has suggested Eared Grebes in North America benefit from nesting close to Franklin's Gulls due to the ability to anchor their nests to gull nests, and thus reduce negative impacts of wind and waves (Burger and Gochfeld 1995). Thus, one might expect Eared Grebes to nest closer to gulls than expected by chance, which is what I found at two of four subcolonies that hosted both species. Burger and Gochfeld (1995) noted that as many as seven Eared Grebe nests could be anchored to a single gull nest, although the number was typically between one and three. I also observed, based on imagery and ground surveys, that a cluster of grebe nests would often surround a gull nest, especially at the subcolonies at Foam Lake where vegetation density was greater. Interestingly, at the one subcolony with the lowest vegetation density (subcolony A, Table 1), grebes nested significantly further from gulls than expected. Perhaps in areas with more open water, grebes are forced to select nest sites wherever there are patches of suitable habitat, irrespective of the presence of gulls. In contrast, Western Grebe nests did not cluster with Franklin's Gulls nests at either of the subcolonies where they co-nested. Since this species is not known to anchor its nests to those of other species, it is possible that simply nesting within the same colony, rather than necessarily nesting closer to gulls within the colony, provides the primary anti-predator advantage that drives Western Grebes to co-nest with gulls. Indeed, few studies have shown that nest success in co-nesting species declines as a function of distance to 'protector' species per se, and those that do mostly include species nesting in association with raptors (Quinn and Kokorev 2002, Mönkkönen et al. 2007, Quinn and Ueta 2008).

As predicted, greater vegetation density at subcolonies was associated with smaller intraspecific nearest neighbor distances, a finding that has previously been noted in Franklin's Gulls and Eared Grebes (Burger 1974a, Boe 1994). Burger (1977) further described this association in four other *Larus* species and suggested that it was related to visibility, whereby under reduced visibility, generally associated with greater vegetation density, neighbors are able to nest closer together without this resulting in overly negative impacts of aggression. Indeed, experimental removal of vegetation confirmed increased neighbor-neighbor aggression in three of the species, including Franklin's Gulls (Burger 1977). Boe (1994) similarly suggested visual protection from neighbors as the mechanism behind smaller neighbor distances with greater vegetation density in Eared Grebe colonies, although this was not demonstrated through observation or experiment. An alternative explanation, also noted above, is that individuals nesting in colonies with more open water may sometimes be forced to nest wherever there is suitable vegetation, instead of being able to choose to nest near conspecifics. Nearest neighbor distances were also smaller at larger subcolonies, which was independent of the effect of vegetation density. The same trend was noted in studies of Western, Silvery, and Rolland's grebes, although no causal explanations were suggested (Burger 1974b, Lindvall and Low 1982). According to the ideal free distribution (IDF, Fretwell and Lucas 1969), larger colonies (i.e., those with more conspecific nesting pairs) may represent higher-quality habitats and allow individuals to nest in greater densities, while maintaining equivalent fitness to individuals nesting in lower-quality, less densely packed colonies. Sachs et al. (2007) provided strong evidence that higher fitness in colonial versus solitary-nesting Red-necked Grebes was due to the higher quality of those nesting habitats, although this does not directly support the IDF due to the differences in fitness across habitats. Another possibility is that increased social attraction favors individuals settling in colonies that are already large (Burger 1988). Disentangling these possibilities in Franklin's Gulls and Western and Eared grebes would require more intensive studies of behavior and fitness at colonies of varying sizes and habitat types - information that would be difficult to obtain from drone surveys alone.

CONCLUSION

Recent work on using drones to survey colonial waterbirds has focused on obtaining nest counts or evaluating relative disturbance (e.g., Magness et al. 2019, Barr et al. 2020, Jones et al. 2020, McKellar et al. 2021), with some limited research aimed at obtaining nest success information (Sardà-Palomera et al. 2017, Lachman et al. 2020). Here I made use of high-resolution imagery taken at difficult-to-access mixed-species marsh bird colonies to test predictions related to nest dispersion. This method allowed for a large sample of nests to be evaluated at multiple subcolonies with minimal disturbance to nesting birds. Future avenues of research for these species could make use of multiple drone flights throughout the nesting season to examine dynamics of colony formation and nest survival in relation to habitat structure and location within the colony (Sardà-Palomera et al. 2017), although the level and accuracy of detail on nesting success that can be obtained from drones alone has been criticized (Callaghan et al. 2018). Nonetheless, such information, obtained from drones with potential supplementary ground surveys, could allow for a better understanding of the highest quality habitats that would benefit from protection for declining and sensitive species.

Responses to this article can be read online at:
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Data Availability:

The data supporting the findings of this study are available upon reasonable request from the author. None of the data are publicly available due to data sensitivity (locations of migratory bird nests).

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