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Importance of Proximity to Foraging Areas for the Pacific Great Blue Heron (*Ardea herodias fannini*) Nesting in a Developed Landscape

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Abstract.—Habitat loss due to human development is a threat to colonial waterbird species, which require nesting habitat in proximity to productive aquatic foraging areas to ensure reproductive success. When development of habitat occurs, waterbirds must either tolerate the changes or relocate nesting colonies to habitat elsewhere. Land cover and nesting colony data were used to study the implications of development for the Pacific Great Blue Heron (*Ardea herodias fannini*). Colonies were closer to major foraging areas than expected by chance, but were not farther from human development than expected by chance, suggesting that Pacific Great Blue Herons will tolerate some development to remain close to major foraging areas. There was no relationship between distance to human development and colony productivity; however, distance to major foraging area was a significant predictor of productivity, which suggests Pacific Great Blue Herons may prioritize proximity to foraging areas because it is critical for reproductive success. Given their demonstrated preference for proximity to foraging areas, and high levels of development near these areas, relocation away from human development may not be an option for nesting Pacific Great Blue Herons in south coastal British Columbia, Canada, because potential nesting habitat availability was most restricted within 5 km of major foraging areas. Future management strategies for this species, and colonial waterbirds in general, should prioritize conservation of nesting habitat near major foraging areas to maximize future reproductive success. *Received 1 September 2015, accepted 16 October 2015.*

Key words.—*Ardea herodias fannini*, colonial nesting, development, foraging area, Great Blue Heron, habitat loss, productivity, waterbird.

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Colonial waterbirds are vulnerable to human development because the habitats they use for nesting and foraging, such as large coastal estuaries, are also home for much of the world's human population (Kennish 2002). When development occurs in or near their habitat, waterbirds must either tolerate the changes or relocate if suitable nesting and foraging habitat is available elsewhere. Waterbirds have been shown to tolerate the disturbance stimulus associated with human presence (Nisbet 2000; Walker *et al.* 2006; Vennesland 2010), but have also been shown to prefer colony locations away from human development (Gibbs *et al.* 1987; Watts and Bradshaw 1994; Gibbs and Kinkel 1997). Furthermore, human presence has been negatively associated with waterbird colony productivity (Tremblay and Ellison 1979; Anderson 1988; Vennesland and Butler 2004; Ellenberg *et al.* 2006).

Colonial waterbirds are particularly vulnerable to habitat loss because they require arboreal nesting habitat in proximity to aquatic or marine foraging habitat (Parnell *et al.* 1988). Foraging area is a primary determinant of waterbird colony location (Gibbs *et al.* 1987; Butler 1997) because proximity to foraging relates energetically to reproductive success (Gibbs 1991; Kelly *et al.* 2008). A colony can be associated with a single main foraging habitat (Forbes *et al.* 1985), and waterbird colony size has been positively related to the amount of foraging habitat available (Farinha and Leitão 1996; Gibbs and Kinkel 1997).

The subspecies of the Great Blue Heron that occurs on the northwest coast of North America, *Ardea herodias fannini* (known as the Pacific Great Blue Heron), provides an ideal case study for colonial waterbird response to human development. The Pacific Great Blue Heron is federally listed as a species of Special Concern under the Canadian Species at Risk Act due to documented declines in nesting productivity, the potential for population declines, and the effects of human and predator disturbance (Committee on the Status of Endangered Wildlife in Canada 2008). The majority of the Canadian population of the Pacific Great Blue Heron nests in treed areas around the tidal mudflats, wetlands, and riverbanks associated with the Fraser River in south coastal British Columbia (Butler 1997), which is also home to approximately 3 million people, and many areas suitable for nesting have been lost to urbanization and rural development such as farms. Although Pacific Great Blue Herons have been shown to tolerate some human activity near their nesting areas (Vennesland 2010), documented declines in nesting productivity are thought to be due in part to disturbance from human activity (Butler 1997; Vennesland and Butler 2004).

In this study, we used records from a long-term dataset of Pacific Great Blue Heron colony surveys to examine the impacts of human development on a colonial waterbird. First, we asked whether the Pacific Great Blue Heron was tolerating human development by comparing the location of nesting colonies to random locations within available nesting habitat in south coastal British Columbia. Second, we explored the consequences of human development to colony productivity by analyzing the impact of colony distance to major foraging areas and areas developed by humans. Third, we measured the amount of remaining habitat for Pacific Great Blue Herons in the study area to assess whether relocation is a viable option for future colonies.

METHODS

Study Area

The study was conducted on the south coast of British Columbia, Canada, in and adjacent to the city of Vancouver (Fig. 1). The study area was defined as the extent of land cover available for Metro Vancouver and the Fraser Valley Regional District. The Fraser River

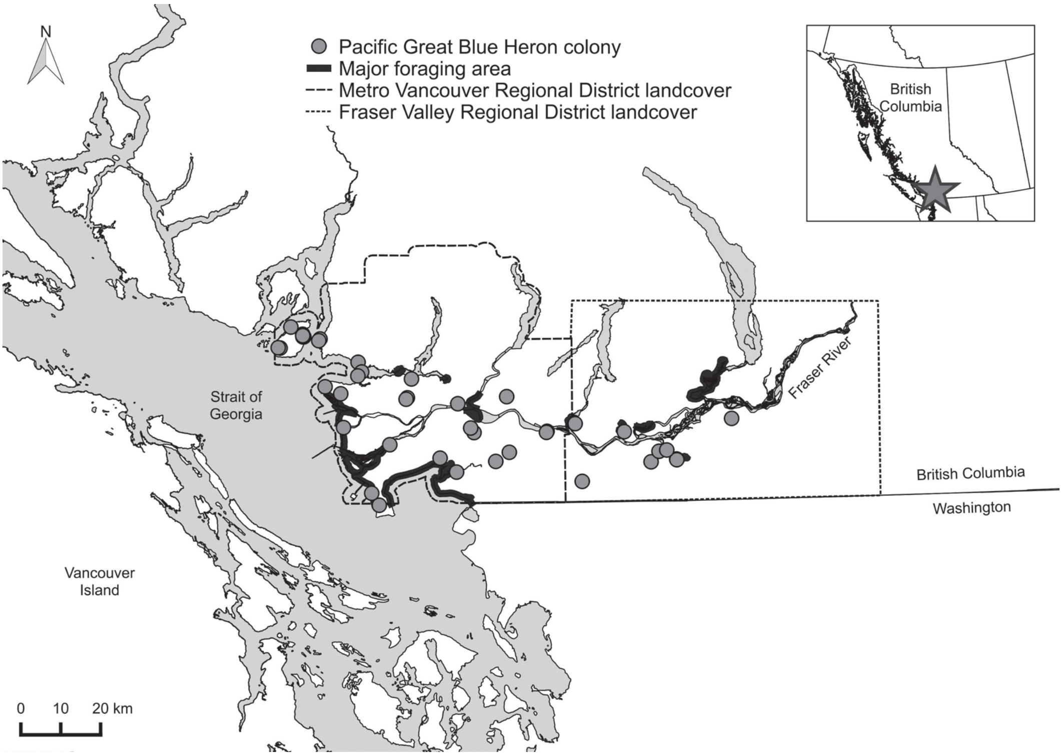

Figure 1. Distribution of Pacific Great Blue Heron colonies and major foraging areas associated with the Fraser River in south coastal British Columbia. The study area was defined as the extent of land cover available for Metro Vancouver and the Fraser Valley Regional District.

runs through the study area and empties into the Pacific Ocean via the Strait of Georgia, where the river provides rich intertidal foraging areas characterized by mudflats and eelgrass (*Zosterina* spp.) beds (Butler 1997). The study area is in the coastal western hemlock biogeoclimatic zone (Meidinger and Pojar 1991). Red alder (*Alnus rubra*) and black cottonwood (*Populus trichocarpa*) are the primary trees used for nesting, although many other tree species are occasionally used as well (Butler 1997; Gebauer and Moul 2001).

Colony Surveys

Data used in our analyses were obtained from a long-term dataset of Pacific Great Blue Heron colony surveys available from the Great Blue Heron Management Team (2013) in British Colombia, Canada. Colony locations were identified through a variety of sources including private landowners, naturalist groups, government agencies, academic research, and thorough vanishing bearing surveys from major foraging areas in 2002 and 2003 (Kenyon 2006). For colony surveys, standardized survey and data handling methodologies were used (Moul *et al.* 2001; Vennesland and Norman 2006). Colonies were typically visited three to five times throughout the nesting season to collect colony productivity data. Visits were timed between 1 April and 31 July to ensure all nesting attempts were adequately documented during surveys. Surveys were conducted by biologists trained in Pacific Great Blue Heron colony survey techniques to maximize data precision and minimize disturbance to nesting birds. Individual nests were tracked to facilitate monitoring over the course of the nesting season. All nests were monitored at colonies with less than 25 nests, and a random sample of nests was monitored at colonies with greater than 25 nests. The activity of the parents and the status of the brood were recorded on each visit, in addition to monitoring predation and disturbance events. At the end of each survey season, summary data were compiled in a long-term database, including total number of active nests, total number of successful nests (i.e., nests that produced fledglings), and total number of fledglings (defined as the maximum number of nestlings observed when the nestlings were at least 4-6 weeks old). Analyses included surveys from 1997-2012 to ensure data were collected using only standardized survey methods.

Identification of Potential Nesting Habitat and Major Foraging Areas

We identified areas of potential nesting habitat from existing land cover data of the Fraser Valley and Metro Vancouver Regional Districts (Fig. 1). Land cover data for the two regional districts were obtained from provincial government sources at pixel resolutions of 5 m^2 and 25 m^2 and derived from LandSat imagery circa 2006 and 2002, respectively, as well as SPOT imagery from 2004 for the Fraser Valley Regional District (Gray *et al.* 2002; Caslys Consulting Ltd. 2007). We defined a patch of potential Pacific Great Blue Heron nesting habitat as continuous treed land cover with no roads or buildings. Since Pacific Great Blue Herons show little preference for nest tree species or age (Gebauer and Moul 2001), all treed areas were included as potential nesting habitat. We then cut the tree layers with a provincial road layer to ensure each habitat patch was continuous and did not include any paved or unpaved roads. We used the minimum patch size of large historical colonies (1,000 m^2) as minimum patch size to ensure potential nesting habitat was suitable for colonies of all sizes. Herons in British Columbia are known to nest below 1,100 m elevation, so we omitted all habitat below 1,100 m (Campbell *et al.* 1990). Finally, we restricted potential nesting habitat to within 15 km of major foraging areas based on an energy restriction calculation (Committee on the Status of Endangered Wildlife in Canada 2008).

We identified major foraging areas by compiling areas identified in previous comprehensive studies of groups (> three individuals) of Pacific Great Blue Heron foraging in the study area (Butler 1995; Kenyon 2005). We then mapped the extent of the riparian or estuarine area at each of those locations by hand as polylines over 2004 orthophotography (Integrated Mapping Technologies, Inc. 2004; Fig. 1).

Distance to Foraging Area and Human Development

We calculated distance to nearest major foraging area (F) and to nearest human development (D) of Pacific Great Blue Heron colonies and random points within the layer created for available nesting habitat (n = 171). We measured F by calculating the distance to the nearest major foraging area automatically in a GIS. We measured D by overlaying colony locations and random points on available orthophotography and measuring the distance to the nearest human area. Human areas were defined as all public roads, all buildings, railroads, industrial areas, and airports. The analysis included only colonies that were active during a year for which high-resolution orthophotography was available ($n = 41$). We found no change in D over time for a subset ($n = 18$) of colonies for which there were multiple years of aerial photography available (1995, 1999, 2004; Triathlon Mapping Corporation and Selkirk Remote Sensing Ltd. 1995; Integrated Mapping Technologies, Inc. 1999, 2004), and the remaining 23 colonies were active for a mean of 2.17 years (maximum 4 years), so we assumed that D was accurate over the lifetime of each colony included in the analysis. We assumed that F did not change over time.

Statistical Analysis

All analyses were conducted at the colony level to avoid pseudo-replication. Colony size was calculated as the total number of active nests observed over the surveyed duration of the colony divided by the number of years surveyed. We also separated Pacific Great Blue Heron colonies into three size classes using Jenks natural breaks in the distribution of colony size (Jenks 1967). Small colonies had less than 39 active nests per year, medium colonies had between 39 and 139 active nests per year, and large colonies had at least 140 active nests per year. All statistical analyses were performed in statistical program R with an $\alpha = 0.05$ (R Development Core Team 2014). Spatial analyses were performed using ArcMap (Environmental Systems Research Institute 2008), and maps for publication were created in the GIS program QGIS (QGIS Development Team 2015).

Colony location. To determine whether colonies were tolerant of development, we compared F and D of Pacific Great Blue Heron colonies to randomly selected locations using two-tailed independent t-tests. We also used one-way analyses of variance (ANOVA) and Tukey's post-hoc tests to test for differences in F and D between the three colony size classes and random. Distance to nearest major foraging area (F) and to nearest human development (D) were square root transformed and natural log transformed, respectively, to satisfy parametric statistical assumptions.

Colony location and productivity. To test for any effects of potential tolerance to human development on colony productivity, we analyzed the influence of D and F on colony productivity for the subset of colonies for which D was calculated ($n = 41$). Productivity was calculated as the total number of fledglings observed over the surveyed duration of the colony divided by the total number of nests monitored over the surveyed duration of the colony. We used this mean colony productivity metric as opposed to a per capita metric because we were interested in the effect of colony-level factors that did not change over the lifetime of a colony. Our mean colony productivity data were zero-inflated due to several colonies that were only active for 1 year and did not produce any fledglings. We, therefore, used hurdle models to analyze the effect of F and D on mean colony productivity. Using a hurdle model also allowed us to test whether total colony failure (i.e., no fledglings produced) and colony productivity were influenced by different parameters. First, we used a binomial generalized linear model (GLM) to test for the influence of F and D on total colony failure. Next, we used a truncated gaussian GLM to test for the influence of F and D on the mean colony productivity of all colonies with mean colony productivity greater than zero. We added mean colony size, the interaction term between mean colony size and F, and the interaction term between mean colony size and D to both models to control for the potential effect of colony size. Each global model was competed against an *a priori* selection of simpler models. We selected the best model using Akaike Information Criterion values corrected for small sample sizes (AIC_c; Burnham and Anderson 2002). To examine the influence of each variable, we calculated the relative variable importance (RIV) by summing the Akaike weights (w_i) of the models containing the common variable. To account for unequal numbers of models between the variables, we divided the RIV by the number of models for each variable to produce an average RIV for each variable (e.g., Kittle *et al.* 2008). We tested for spatial autocorrelation of mean colony productivity using semi-variograms of all data and of only colonies with mean colony productivity greater than zero (Dormann *et al.* 2007). We found no trend in semi-variance in either data set and, thus, did not account for spatial autocorrelation in our analysis.

Nesting habitat availability. We quantified potential Pacific Great Blue Heron nesting habitat by distance to a major foraging area (< 5 km, 5-10 km, > 10-15 km). For each distance category, we calculated amount of nesting habitat, and the proportion of habitat to overall area in that distance category. We also tested habitat availability in relation to major foraging areas by comparing F of random treed points to F of random points within developed areas (as classified in the land cover data) using a Mann-Whitney U-test.

RESULTS

Colony Location

Pacific Great Blue Heron colonies were located between 0.4 km and 17.9 km from the nearest major foraging area (F), with a mean F of 7.0 km (SD = 5.7 km). Overall, Pacific Great Blue Heron colonies were not closer to major foraging areas than expected by chance ($t_{48.3} = -1.44$, $P = 0.16$; Fig. 2). We found a difference in the distance to major foraging area between random points and the three colony size classes, and a Tukey's post-hoc test revealed that medium (39 to 139 nests) and large (> 139 nests) size classes were significantly closer to major foraging areas than random ($P \leq 0.01$), but small colonies (< 39 nests) were approximately equidistant from foraging areas as random (8 km; $P = 0.99$). Medium and large colonies were, therefore, also closer to major foraging areas than small colonies ($P = 0.06$).

Distance to human development (D) was less than 400 m for all Pacific Great Blue Heron colonies included in the analysis, with a mean D of 80 m (SD = 97 m). Some colonies ($n = 10$) were directly adjacent human development (i.e., $D < 10$ m), including areas of frequent activity such as public parks and parking lots. The most common types of human development near colonies were roads ($n = 18$) and houses ($n = 16$); however, many colonies were near multiple types of development. Pacific Great Blue Heron colonies were significantly closer to human development than random ($t_{65.9} = -6.10$, $P < 0.001$; Fig. 2); however, post-hoc analysis showed that this trend was driven by small colonies, which were the only colonies significantly closer to human development than random ($P < 0.001$).

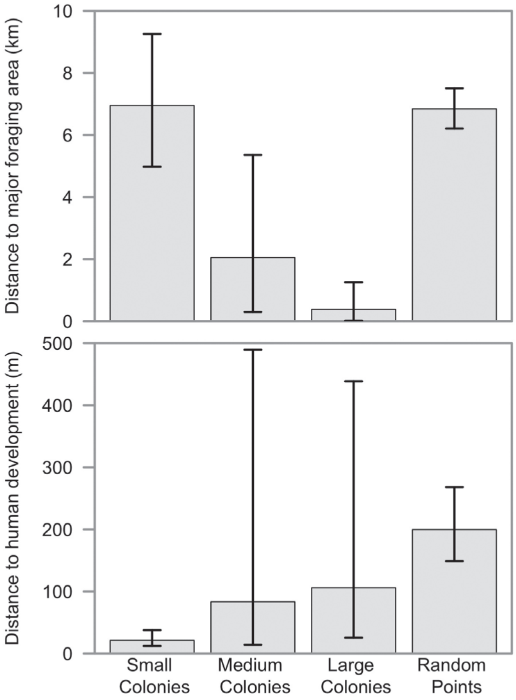

Figure 2. Distance to major foraging area (*F*) and human development (*D*) of Pacific Great Blue Heron colonies and random points within potential nesting habitat. Variables were back transformed from square root and natural log, respectively. Errors bars represent 95% confidence intervals.

Colony Location and Productivity

The overall mean colony productivity was 1.06 fledglings per nest (SD = 0.73), with minimum and maximum mean colony productivity of 0 and 2.63 fledglings per nest, respectively. Eight of the 41 Pacific Great Blue Heron colonies included in the analysis were single-year colonies that failed and therefore produced zero fledglings (total colony failure). None of the models of total colony failure were strongly supported, although there was some indication that total colony failure was more common in smaller colonies. The model including only colony size was the top model, and the average RIV for colony size was greater than for *F* and *D* (average RIV = 0.11, 0.09, and 0.06, respectively); however, the term for colony size was not significant in any of the models (all $P > 0.10$; Table 1).

Of the 33 colonies that produced fledglings, mean colony productivity was 1.32 fledglings per nest (SD = 0.54). For those colonies that produced fledglings, there was strong support for the model including only *F* ($w_i = 0.51$), and *F* was included in the top three models (Table 1). The average RIV of *F* was higher than of *D* and colony size (average RIV = 0.14, 0.04, and 0.04, respectively). The top model including only *F* predicted that mean colony productivity was reduced by 0.04 fledglings per nest for every km away from a major foraging area (Fig. 3). There was no model support for an influence of *D*, colony size, or the relationship between colony size and *F* or *D* on productivity.

Nesting Habitat Availability

Potential Pacific Great Blue Heron nesting habitat was significantly farther from major foraging areas than developed areas ($U_{247,199} = 71622.0$, $P < 0.001$). Potential nesting habitat was most restricted within 5 km of major foraging areas, and habitat availability increased with increased distance from major foraging areas (Table 2). In particular, potential habitat was most restricted around the intertidal mudflats where the Fraser River empties into the Strait of Georgia (Fig. 4).

DISCUSSION

The colony location choice of Pacific Great Blue Herons in the developed areas of south coastal British Columbia suggests that colonial waterbirds will tolerate human development under some circumstances to remain close to major foraging areas, thereby emphasizing the importance of foraging areas to breeding waterbirds. Medium (39-139 nests) and large (> 139 nests) heron colonies were located closer to major foraging areas than expected by chance, despite analysis that showed nesting habitat availability was most restricted near those major foraging areas. Small colonies (< 39 nests) were located closer to human development than expected by chance, when analyzed by colony size class, while medium and large colonies were not farther from human development than expected by chance. Other studies of Great

Table 1. AIC_c ranking of models of Pacific Great Blue Heron colony failure and mean colony productivity. *F* is the distance from a Pacific Great Blue Heron colony to the nearest major foraging area, and *D* is the distance to the nearest human development.

Model	*N*	*K*	ΔAIC_c	w_i
Total colony failure				
Fate = Colony Size	40	2	0.00	0.25
Fate = *F*	40	2	0.78	0.17
Fate = *F* + Colony Size	39	3	1.05	0.15
Fate = *D* + Colony Size	39	3	1.67	0.11
Fate = *D* + Colony Size + *D*: Colony Size	38	4	1.85	0.10
Fate = *F* + Colony Size + *F*: Colony Size	38	4	2.52	0.07
Fate = *F* + *D* + Colony Size	38	4	2.86	0.06
Fate = *F* + *D*	39	3	3.12	0.05
Fate = *F* + *D* + Colony Size + *F*: Colony Size + *D*: Colony Size	36	6	4.60	0.02
Fate = Null	41	1	4.90	0.02
Fate = *D*	40	2	6.23	0.01
Colony productivity				
Productivity = *F*	31	2	0.00	0.51
Productivity = *F* + *D*	30	3	2.56	0.14
Productivity = *F* + Colony Size	30	3	2.57	0.14
Productivity = Null	32	1	4.38	0.06
Productivity = *F* + Colony Size + *F*: Colony Size	29	4	4.98	0.04
Productivity = *F* + *D* + Colony Size	29	4	5.31	0.04
Productivity = Colony Size	31	2	5.49	0.03
Productivity = *D*	31	2	6.10	0.02
Productivity = *D* + Colony Size	30	3	7.75	0.01
Productivity = *D* + Colony Size + *D*: Colony Size	29	4	9.20	0.01
Productivity = *F* + *D* + Colony Size + *F*: Colony Size + *D*: Colony Size	27	6	10.72	0.00

Blue Heron colony location have consistently found that colonies were further from human development (Gibbs *et al.* 1987; Watts and Bradshaw 1994; Gibbs and Kinkel 1997). The partial discordance between our results and previous studies may be an artifact of the high level of human development that we identified near the major foraging areas in our study area. Pacific Great Blue Herons breeding in the study area may be forced to select colony sites near human development to remain near major foraging areas because major foraging areas are surrounded by human development.

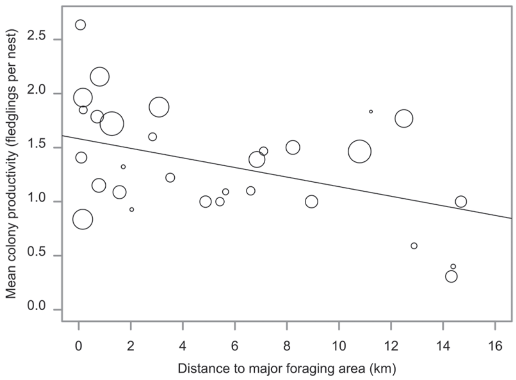

Figure 3. Distance to major foraging area (*F*) and mean colony productivity of Pacific Great Blue Heron colonies that produced fledglings from 1997 to 2012. Point size is proportional to the mean number of nests at each colony over the surveyed duration of the colony.

The importance of foraging area to Great Blue Heron reproductive success is supported by our analysis of reproductive success, which showed that mean Pacific Great Blue Heron colony productivity was significantly predicted by distance to major foraging area. A positive relationship between proximity to foraging area and reproductive success has been previously shown for a variety of avian species (Simpson *et al.* 1987; Frey-Roos *et al.* 1995; Boersma and Rebstock 2009). Although it is possible that Pacific Great Blue Herons in small colonies may have foraged in smaller, less rich areas that were not identified in this study, neither colony size nor

Table 2. Amount of Pacific Great Blue Heron potential nesting habitat near major foraging areas in south coastal British Columbia. Fifteen km is the distance at which the energetic cost of flight is estimated to require 90% of foraging intake that could be provisioned to young.

Distance to Major Foraging Area (km)	Amount of Potential Habitat (km^2)	Proportion of Total Area (%)
< 5	560.0	38.8
5-10	756.6	51.4
> 10-15	661.6	56.3

the interaction between colony size and distance to foraging area was related to mean colony productivity. In contrast, DesGranges (1979), Forbes *et al.* (1985), and Vennesland and Butler (2004) found a positive relationship between Great Blue Heron productivity and colony size, and Vennesland and Butler (2004) and Kelly *et al.* (2007) have previously shown that smaller colonies fail more often. The discrepancy between our work and previous studies is likely because we used colony lifetime metrics that decoupled the link between colony size and productivity that has been shown through analysis of annual metrics.

We found no relationship between distance to human development and mean colony productivity. Reviews have suggested that human activity negatively affects nesting in waterbirds (Parnell *et al.* 1988) and in Great Blue Herons (Vennesland and Butler 2011). Studies on Great Blue Herons and other waterbirds have found that human activity had a direct negative impact on nesting productivity (e.g., colony abandonment; Bjorklund 1975; Vennesland and Butler 2004) or an indirect negative impact on nesting productivity (e.g., increasing predation; Simpson and Kelsall 1979; Tremblay and Ellison 1979). Consequently, it would be

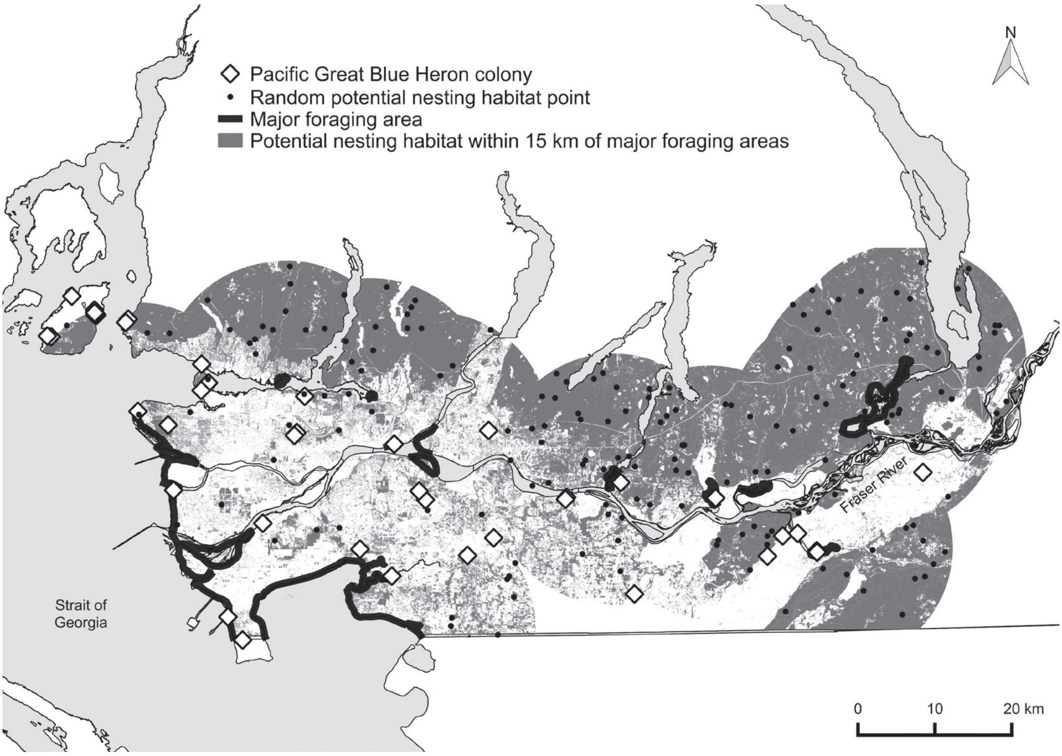

Figure 4. Potential nesting habitat for the Pacific Great Blue Heron within 15 km of major foraging areas in south coastal British Columbia.

expected for colonies near to human activity to have lower nesting productivity, but our study found no relationship between nesting productivity and the proximity of human development, perhaps because low variation in distance to development made it difficult to detect a relationship. Both the overall mean colony productivity (1.06 fledglings per nest) and mean colony productivity of successful colonies (1.32 fledglings per nest) were lower than productivity reported for Great Blue Herons in less developed areas (2.17 fledglings per nest; Carlson and McLean 1996), but also for other highly developed areas (1.93 fledglings per nest; Kelly *et al.* 1993). Particularly low mean colony productivity in our study area may also be attributed to high depredation rates by the Bald Eagle (*Haliaeetus leucocephalus*), which could mask the effect of human development on Pacific Great Blue Heron productivity (Vennesland and Butler 2004). Another explanation for the lack of relationship between proximity to human disturbance and mean colony productivity may be that not all human activity negatively affects nesting productivity because some human activity is relatively benign (Nisbet 2000). For example, several studies have found that waterbirds respond less to the presence of routine mechanical devices such as cars and boats than pedestrians (Rodgers and Smith 1995; Carlson and McLean 1996; Vennesland 2000), presumably because they provide less of a threat. Our measure of human activity was based on built structures, which do not necessarily disturb nesting herons, whereas previous studies have used more specific measures of human activity such as the rate of pedestrian activity adjacent to colonies (Vennesland and Butler 2004). A final alternative may be that the productivity metric used here (mean productivity over the lifetime of the colony) is not adequately sensitive to the effects of distance to development because it combines nest survival (fledge or fail) with productivity of successful nests.

The persistence of Pacific Great Blue Herons in a developed area near major foraging areas, despite low nest productivity and high levels of human development, suggests the study area remains valuable nesting habitat. Pacific Great Blue Herons nesting in the study area may be hesitant to relocate colonies elsewhere because proximity to major foraging areas is critical for reproductive success. The possibility remains that some small colonies went undetected in the less populated portions of our study area; however, this would not have affected our results, which showed that distance to major foraging area and distance to human disturbance of small colonies were similar to random.

Conservation of a complex of treed nesting habitat and rich foraging areas is critical for sustaining colonial waterbird populations, given the documented importance of foraging area for nesting colonial waterbirds shown here and elsewhere (Gibbs 1991; Kelly *et al.* 2008). In developed areas, the traditional conservation approach for colonial waterbirds has been to protect the location of individual colonies and buffer them from disturbance, but this strategy is risky and near-sighted for many waterbirds because colonies relocate over time (Vennesland and Butler 2011). Although continued buffering of existing sites from disturbance is crucial for short-term conservation (Bjorklund 1975; Vennesland and Butler 2004), we also recommend that a landscape scale approach for colonial waterbird habitat protection is critical for long-term conservation (Friesen 1997; Gebauer and Moul 2001; Kenyon *et al.* 2007; Kelly *et al.* 2008). We further recommend that landscape conservation efforts recognize the habitat preferences shown here and consider prioritizing distance to major foraging areas over absence of human disturbance when selecting potential conservation areas. Conservation of nesting habitat near major foraging areas is critical for sustaining colonial waterbird populations, as distance to major foraging areas could be a determinant of reproductive success (Kelly *et al.* 2008).

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