

REPRODUCTIVE ECOLOGY OF URBAN-NESTING GLAUCOUS-WINGED GULLS *LARUS GLAUDESCENS* IN VANCOUVER, BC, CANADA

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SUMMARY

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The present study investigated the reproductive success and breeding ecology of 102 Glaucous-winged Gull *Larus glaucescens* pairs nesting in downtown Vancouver, British Columbia during the summer of 2015. These urban breeders enjoyed a remarkably high level of post-hatch fledging success ($\geq 85\%$) compared to previous records for non-urban subpopulations in the region ($\approx 70\%$). A relatively small average initial clutch size of 2.43 eggs was observed, which aligns with a historical analysis of the literature and corroborates the inference that clutch size has declined substantially in the region over the past century. I argue that the high level of post-hatch fledging success is likely attributable to a tendency of urban Glaucous-winged Gulls to establish isolated nesting territories, often on the rooftops of individual buildings, which leads to low intra- and interspecific predation. Given that offspring commonly return to their natal sites to breed later in life, the evolutionary impact of this reproductive differential could be significant for the ecological future of Glaucous-winged Gulls in the region.

Key words: Glaucous-winged Gull, *Larus glaucescens*, reproductive success, urban nesting, rooftop nesting, urban ecology, Vancouver

INTRODUCTION

The Salish Sea is a large network of inland bodies of water and coastal watersheds that stretches from British Columbia's Strait of Georgia south through the Puget Sound in Washington and west to the Strait of Juan de Fuca. Glaucous-winged Gull *Larus glaucescens* populations have declined substantially in this region since the 1980s, from an estimated high of 13 000 nesting pairs in 1986 to an estimated low of 5 600 in 2010 (Sullivan *et al.* 2002, Bower 2009, Blight *et al.* 2015). Changes in food availability and food quality are among the most prominent hypotheses explaining this decline (Blight *et al.* 2015), and both hypotheses are consistent with an observed decrease in the size and overall health of forage fish populations in the Salish Sea (Therriault *et al.* 2009).

To track changes in the size and health of the Glaucous-winged Gull population in the Salish Sea, extensive colony counts have been undertaken over the last 30 years, notably by Vermeer & Devito (1989), Vermeer (1992), and Blight (2012). Special attention has usually been paid to the large colonies on Mandarte Island and Mitlenatch Island in the Strait of Georgia. Nearly all studies have been restricted to nesting pairs in non-urban environments; the only systematic studies of urban-nesters were conducted by Hooper (1988) and Vermeer *et al.* (1988), both in the summer of 1986. Hooper's study was conducted in Victoria, BC, while Vermeer *et al.* focused on downtown Vancouver, BC, the densest urban centre in the region.

Despite many studies documenting the ability of various gull species to adapt to the urban environment (e.g., Dwyer *et al.* 1996, Temby 2000, Rock 2005, Soldatini *et al.* 2008), surprisingly little is known about the urban-specific ecology of most gulls. Outside of the literature concerning the European Herring Gull

L. argentatus in northern Europe (e.g., Monaghan & Coulson 1977, Raven & Coulson 1997, Rock 2005, Balmer *et al.* 2013), virtually nothing is known about the distribution of these species in the urban portions of their ranges. Particularly little is known about their reproductive success and how it differs, if at all, from that of non-urban-nesting conspecifics. In this study, I address the latter issue for the Glaucous-winged Gull. Although reproductive success of urban-nesters was studied once in 1986 in the City of Vancouver (Vermeer *et al.* 1988), substantial pressures have been applied to the region's Glaucous-winged Gull population since that time (Blight 2011). As this species continues to face extra stressors in its original, non-urban environment, it becomes conceivable that an urban setting may offer a type of refuge, especially if the urban environment comes equipped with its own attractive features.

There are many reasons why an urban-nesting population of gulls could enjoy greater reproductive success compared to non-urban-nesting conspecifics. Most obviously, predatory species like the Bald Eagle *Haliaeetus leucocephalus* are often deterred from urban environments due to the extreme human presence (Buehler *et al.* 1991, Steidl & Anthony 2000). More importantly, because the size of one rooftop often allows only a single nest, the practice of rooftop nesting can equip breeding pairs with a structural territorial boundary that cannot be physically breached by any chicks that have not yet learned to fly. This likely results in very low predation rates by other breeding Glaucous-winged Gulls in neighboring territories, though this idea has yet to be formally tested. Chick mortality from neighboring adults has been repeatedly shown to contribute substantially to nesting and reproductive failure in colonially breeding gulls (Hunt & Hunt 1975, Kovacs & Ryder 1983), and particularly among Glaucous-winged Gulls in a non-urban environment (Vermeer 1963, Gillett *et al.* 1975).

The consumption of human garbage seems to have widely variable effects on health and fecundity in gull species (Ward 1973, Vermeer 1982, Pons 1992, Belant *et al.* 1998), and it is not clearly understood how landfills act as attractants or deterrents for different gull species (Rock 2005). It is therefore uncertain if urban-nesting gulls really enjoy greater access to food sources, or if the average quality of these food sources is measurably worse than that of non-urban-nesting conspecifics. While several major landfills exist in the Salish Sea region surrounding Vancouver, the city is also adjacent to the Strait of Georgia and Howe Sound, both of which support rich, though declining, forage fish populations (Therriault *et al.* 2009, Davis *et al.* 2015). It has been prominently noted (e.g., Blight 2011, 2012) that access to lower quality food sources could have a substantial negative impact on the reproductive success of seabird species. Despite the complex interaction of these factors on the population's reproductive ecology, it is at least clear that the region immediately surrounding the City of Vancouver is currently capable of supporting many breeding gulls.

Motivated by several years of casual observation by the author (i.e., not directed toward addressing a specific scientific hypothesis), this study addresses the hypothesis that urban-nesting Glaucous-winged Gulls should exhibit greater reproductive success than their non-urban-nesting conspecifics in the central Salish Sea region. Because gulls often return to their natal sites to breed (especially among male offspring; Reid 1988, Rock 2005) and because breeding pairs show a high amount of nest fidelity (Vermeer 1963), urban vs. non-urban differences could have important implications on species evolution, wildlife management, and conservation efforts.

TABLE 1
Observation sites, number of observable city blocks, number of observable nests, and number of reliably observable nests at each site^a

Observation site	Number of observable city blocks	Number of observable nests	Number of reliably observable nests
555 W. Hastings St. Vancouver Lookout	48	120	77
699 Cardero St. Private residence, 21st floor, NE view	6	22	13
1022 Nelson St. Private residence, 19th floor, SW view	17	15	7
Granville Bridge NW pedestrian walkway	2	4	4
Cambie Bridge SW pedestrian walkway	1	1	1
Total	70	162	102

^a Nests were considered reliably observable only if there existed unobstructed views of the chicks to fledging on at least two distinct occasions. Note that a city block is not a standardized unit of measure. Further, due to disparate building heights relative to the observer's vantage point, not all structures on every surveyed city block were directly observable (see Fig. 1).

METHODS

Study area

The study area was composed of five distinct observation sites in downtown Vancouver, BC. A varying number of city blocks and rooftops were observable from each site (Table 1). Most rooftops were at least partially visible on each observable block at each site; see Fig. 1 for an exact illustration of the observable area. Observation sites were chosen preferentially for ease of access and for the presence of maximal observable roof space within a continuous region of the downtown core. Naturally, a site effect may influence the observations in some way, but all sites were located within a single 1.5 km radius and were comparable in terms of the urban geography, urban density, proximity to the Salish Sea, and proximity to each other.

Nest sites were observed for eggs and hatched young once per week in late May and early June 2015. All observations were conducted from the observation sites listed in Table 1. Once chicks began to hatch, formal counts of brood size were taken regularly between 21 June (the date of first observed hatching) and 15 September. All broods were observed until chicks were at least six weeks old or had lost all their natal down, after which time all surviving chicks were considered fledged. Post-hatch fledging success rates for each brood were calculated as the proportion of fledglings to hatchlings.

All observations were made by the author with a Canon Powershot SX50 HS camera with 50× optical zoom and 200× combined zoom. Observations were passive, in that they did not involve any interaction with the birds.

Survey inclusion criteria

All broods that could be reliably observed (i.e., viewed unobstructed on at least two different occasions) were included

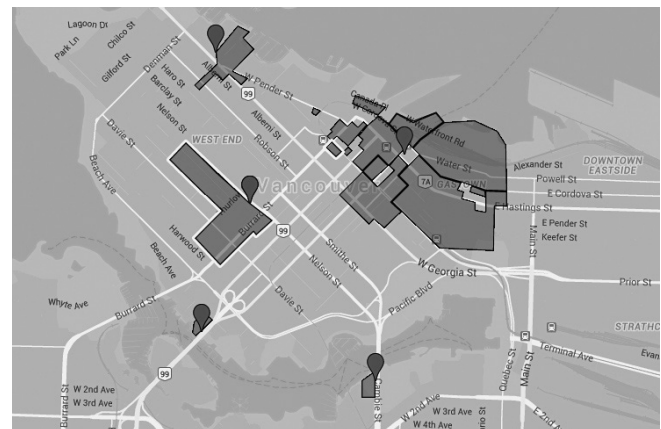


Fig. 1. The observation sites in downtown Vancouver, BC, clockwise from the upper left: 699 Cardero St., 555 W. Hastings St., Cambie Bridge, Granville Bridge, and 1022 Nelson St. Pins indicate the actual location of observation sites. Shaded regions indicate observable city blocks; lighter regions within shaded regions indicate areas that were unobservable (e.g., view blocked). Note that the main study area of Vermeer *et al.* (1988) is adjacent to the Cambie Bridge site, immediately to the east. Map data: copyright 2015 Google.

in the analyzed sample. Some nesting territories were too obscured from the fixed observation sites (Table 1) to allow consistent tracking of chicks; these were omitted from analysis. Other nesting sites were omitted due to nest failure, i.e., no eggs hatched, or the nest was abandoned by the parents before the eggs hatched. Of 162 recorded active nests in the study area, 8 failed and 102 were reliably observable.

Left-censoring of data

While many broods were observed from the time of hatching, some were only discovered several days or weeks after hatching as chicks became more mobile. Some nests were completely obstructed from view (e.g., hidden behind a wall), but because most nesting territories spanned an entire rooftop, chicks became visible from the observation site as they left the nest and began to explore their parents' territory. Observations were conducted only on chicks lacking flight ability, so there was no possibility of mistakenly counting chicks from a neighboring rooftop territory if it was separated by a vertical drop-off (73 of 102 nests; see Results). For rooftops that contained more than one nest, families could be separated by simultaneous observation of all breeding pairs having chicks on their respective territories.

As most chick deaths occur in the first week after hatch (Vermeer 1970, Kovacs & Ryder 1983), this passive methodology introduced an amount of left-censoring into the data, since the number of hatchlings was not always known. Of the 102 nests included in this analysis, I was able to record initial brood sizes for 84 nests.

Post-hatch fledging success is defined as the proportion of fledglings to hatchlings, and it is an important proxy for overall reproductive success. Clearly, the presence of left-censoring in the hatchling data can distort any derivative estimates of post-hatch fledging success. To account for this, I adjusted the counts of broods that were first observed only after all chicks had hatched (18 of 102 broods) as follows: if a terminal clutch size was not determined prior to observation of the chicks and if the observed brood size was two or fewer, the initial brood size was automatically adjusted to three. This means that the true initial brood counts will always lie between the observed and adjusted brood counts. Estimates derived from both the observed and adjusted counts are reported, resulting in upper and lower bounds, respectively, on post-hatch fledging success.

It is important to emphasize that analyzing these adjusted data leads to the construction of minimum estimates of post-hatch fledging success for the sampled population. It is quite possible that some observed broods of size two actually came from unobserved terminal or initial clutches of size two, and thus were unnecessarily adjusted upwards. Nevertheless, the results from this adjusted analysis are in broad agreement with the unadjusted figures, and both lend support to this study's main hypothesis.

Clutch size

Due to the observational limitations discussed above, initial clutch sizes were determinable for only 21 nests in the sample. Consequently, the observed estimate of average initial clutch size is both highly susceptible to sampling variability and, perhaps, sampling bias. To assess the reliability of this estimate, reasonable approximations to the frequency distribution of initial clutch

size counts were derived over the full sample population, by transforming the 102 recorded initial brood sizes.

It is well known that younger gulls are more likely to lay smaller clutches and hatch fewer offspring than older, more experienced conspecifics (e.g., Haymes & Blokpoel 1980). Thus, the relative distribution of initial clutch size will not scale uniformly with the relative distribution of initial brood size. For Glaucous-winged Gulls, Verbeek (1986) suggests that approximately 80% of eggs in three-egg initial clutches hatch, while only about 70% of eggs in two-egg initial clutches hatch. These numbers agree with the recent results of Ross-Smith *et al.* (2015) on the hatching success of the Lesser Black-backed Gull *L. fuscus* in Wales. Consequently, I constructed expected distributions of initial clutch sizes for this study using the hatching success figures of Ross-Smith *et al.* (2015) to scale initial brood size counts appropriately. The exact transformation yielding the expected proportion of *i*-egg initial clutches is as follows:

$$(1) \quad \widehat{CS}(i) := \frac{BS(i)/HS(i)}{\sum_{k=1}^3 BS(k)/HS(k)},$$

where $BS(i)$ denotes the number of observed initial broods of size *i* and $HS(i)$ denotes the hatching success figures of Ross-Smith *et al.*: 0.8 for three-egg, 0.7 for two-egg, and 0.35 for one-egg clutches.

It is impossible to directly validate this post-hoc adjustment without auxiliary data that are unavailable for the present study. However, a simple sensitivity analysis was performed on the choice of Ross-Smith's scaling factors to investigate the precariousness of these adjustments. Varying each scaling factor independently over a range of ± 5 percentage points resulted in sample frequency distributions that differed from the initial one (produced by Equation 1) by no more than ± 2 percentage points for each clutch size. That is, varying the proportion $HS(k)$ by ± 5 independently for each value of k ($= 1, 2, \text{ or } 3$) resulted in a change in the proportion $CS(i)$ of no more than ± 2 for each fixed value of *i*. This demonstrates a relative insensitivity of the expected proportion of initial clutch sizes to the exact choice of hatching-success scaling factor. Moreover, the resulting calculation for average clutch size that was derived from these expected proportions varied by no more than 0.10 when the scaling factors range as above, and by no more than 0.15 when the scaling factors range independently over ± 10 percentage points. Average clutch size is a figure of interest for studies of reproductive success, and one that is used to help compare the results of related studies (see Discussion). The robustness of this derived figure to the exact choice of scaling factors increases confidence in the associated qualitative content.

RESULTS

The first observed hatching occurred on 21 June and the last occurred on 22 July, with most hatchings completed by 04 July. The first observed fledging occurred on 04 August, and the last was on 15 September.

Observed numbers of nesting pairs and fledglings are categorized by initial observed brood size and are displayed in the first three rows of Table 2, while the same counts, adjusted for left-censoring, are displayed in the last three rows. Of the 84 broods where initial brood size was known, 66 had three chicks, 14 had

two, and 4 had one. Left-censored counts were evident in 18 broods, and all were changed to the maximum initial brood size of three in the adjusted counts.

Post-hatch fledging success is calculated as the proportion of fledglings to hatchlings. Both the unadjusted and the left-censored adjusted data show high post-hatch fledging success rates across all initial brood sizes (75%–94%). The unadjusted overall post-hatch fledging success rate was observed to be 93% (95% binomial confidence interval: 89%–96%). The adjusted overall post-hatch fledging success rate was observed to be 85% (95% binomial confidence interval: 81%–89%). Consequently, 85% is a *lower bound* on the true post-hatch fledging success rate of the sample.

Of the 102 nests included in this study, 73 were situated as solitary nests on isolated rooftops or structures, and no more than 7 nests were located on a single contiguous surface. (These seven nests were on the old Canada Post helipad at 349 W. Georgia Street.) Solitary nest sites ranged in size from < 2 m² (e.g., the rooftop of a stairwell landing) to > 10 000 m² (e.g., the entire rooftop of a large building). No nest was observed < 5 m above the ground, while one nest was observed atop a building of > 100 m in height. Among 102 nests, 87 were built between 10 and 45 m above ground-level, with a quarter of those built between 25 and 30 m above ground level. Two nests were built atop pedestrian walkways spanning busy traffic corridors, two or three stories above the street (see Fig. 2).

Egg predation by gulls was not recorded during the informal observation phase from late May to early June. No chick deaths due to attacks from adult gulls were directly observed (compare with Good 2002). A single chick death was observed due to predation from a Bald Eagle. There was no systematic observational or sampling framework in place to track post-fledge fatalities; a small number of fledged chicks in the downtown core were incidentally observed to be killed by automobile traffic, although it is unknown how many (if any) were members of the sample population.

At least 69% of observed Vancouver-resident pairs raised all their chicks to fledging, 21% lost one chick before fledging, 7% lost two chicks before fledging, and 3% lost all their chicks prior to fledging (adjusted data, Fig. 3). It should be noted that these success rates are aggregate over all initial brood sizes.

As indicated in the Methods, there was no observer interaction with sample subjects. Consequently, it was possible to observe initial clutch sizes only for nests that were both sufficiently unobstructed and close enough to respective observation sites (Table 1). Initial clutch sizes were directly observed for 21 nests: 1 (of 1) at Cambie Bridge, 4 (of 4) at Granville Bridge, 8 (of 13) at Cardero St., 5 (of 7) at Nelson St., and 3 (of 77) at Hastings St. The low observation rate for the Hastings site was caused by the great distance from which observations were made (50 m to more than 1000 m away from the Observation Deck of the Vancouver Lookout Tower). Of these 21 observed nests, there were 2 initial clutches of one egg, 8 initial clutches of two, and 11 initial clutches of three, yielding an average initial clutch size of 2.43 eggs (approximate 95% normal confidence interval: 2.14–2.72).

Applying Equation 1 to the raw data resulted in an average initial clutch size of 2.39 eggs; applying it to the left-censored adjusted data yielded an average initial clutch size of 2.69 eggs (Table 4).

DISCUSSION

Extent of left-censoring

I have already described why some amount of left-censoring is almost surely present in the raw observed data. The proposed adjustment (see Methods) ensured that the true, possibly unobserved, initial brood count always lay between the observed and adjusted counts, inclusively. While working with the adjusted count has the theoretical advantage that all estimates of post-hatch fledging success are guaranteed to be lower bounds on the true rate in the

TABLE 2
Aggregate post-hatch fledging success rates across all observation sites^a

Initial Brood Size (unadjusted)	Number of Pairs	Number of Fledglings	Fledglings Per Pair	Post-Hatch Fledging Success
3	66	183	(2.63) 2.77 (2.87)	(88%) 92% (96%)
2	27	51	(1.69) 1.89 (1.98)	(85%) 94% (99%)
1	9	8	(0.52) 0.89 (0.99)	(52%) 89% (99%)
total	102	242	-	(89%) 93% (96%)
Initial Brood Size (adjusted)	Number of Pairs	Number of Fledglings	Fledglings Per Pair	Post-Hatch Fledging Success
3*	84	213	(2.38) 2.54 (2.66)	(79%) 85% (89%)
2*	14	26	(1.53) 1.86 (1.98)	(77%) 93% (99%)
1*	4	3	(0.30) 0.75 (0.95)	(19%) 75% (99%)
total	102	242	-	(81%) 85% (89%)

^a Figures in unstarred rows are reported as observed. Figures in starred rows have been adjusted to account for left-censoring of the observational data: if a terminal clutch size was not determined prior to observation of the chicks and if the observed brood size was two or less, then the adjusted initial brood size was set to three. This procedure produces estimates of minimum post-hatch fledging success. Of the 102 observed clutches, 18 were left-censored. Point estimates of fledgling rates per pair and post-hatch fledging success are flanked by binomial 95% confidence intervals in parentheses.

sample, it is natural to ask just how close these lower bounds are. The suspiciously high post-hatch fledging success figures associated with the raw count data highlight the significance of left-censoring, indicating that the true post-hatch fledging success rate of the sample may be better captured by the adjusted figures in Table 2.

Clutch size

The small number (21) of observed initial clutch sizes produced a very uncertain estimate of 2.43 eggs for the average initial clutch size of the sampled population. To reduce the uncertainty in this estimate, 102 counts of initial brood size were scaled using the hatching success factors of Ross-Smith *et al.* (2015) for both the raw and the adjusted data, producing minimum and maximum estimates, respectively, of average initial clutch size: 2.39 and 2.69 eggs. This interpretation holds only if the hatching success factors used in the calculation were accurate for the sample population. As noted in the Methods section, this cannot be known

without auxiliary validation data. However, the sensitivity analysis described in that section lends credibility to the relative robustness of these bounds. The observed estimate of average initial clutch size falls comfortably between these two figures; this should address concerns that the small sample size generating this estimate (i.e., 21 of the 102 study nests) may be subject to a subsampling bias. Thus, while the sampling variability of the initial-clutch-size estimate of 2.43 eggs may still be quite large, the estimate itself appears to capture an accurate measure of average initial clutch size in the full sample population.

The work by Blight (2011, 2012) suggests that the average clutch sizes of breeding Glaucous-winged Gulls in the Salish Sea have declined over the last 35 years, from an average size of about 2.75 to 2.35 eggs per clutch. The present study's estimate of average initial clutch size (2.43 eggs) corroborates this claim. Interestingly, such a decline is also suggested by the relative frequency distributions of initial clutch size presented in Table 3. The main thing to note here is that the distribution of initial clutch sizes is becoming less



(A)



(B)



(C)

Fig. 2. (A) Glaucous-winged Gull chicks at five and a half weeks old, as viewed from the Vancouver Lookout tower. This brood was raised on a narrow ledge surrounding a rooftop 10 stories above Hastings St. (B) A pair of four-week-old chicks at their nest site atop the roof of a pedestrian walkway spanning Seymour St., as viewed from the Vancouver Lookout tower. Chicks were confined to the walkway rooftop, which is built directly out from the sheer walls of the adjoining buildings. (C) Parent, chick, and nest surrounded by owl effigies atop a stairwell landing of a residential building, as viewed from the 699 Cardero St. observation site. Note the presence of bird spikes around the landing rim.

TABLE 3
The sample relative frequency distributions of initial clutch size in *L. glaucescens* across this study and three others containing the requisite information^a (Vermeer 1963, Verbeek 1986, Vermeer *et al.* 1988). The dates provided indicate the year in which the study observations were made.

Initial Clutch Size	Relative Frequencies of Initial Clutch Size				Expected Relative Frequencies	
	(1962) Vermeer Mandarte Is.	(1979–80) Verbeek Mandarte Is.	(1986) V-P-S Vancouver	(2015) Kroc observed	(2015) Kroc adj. scaled	(2015) Kroc raw scaled
3	84%	78%	79%	52%	77%	56%
2	14%	18%	15%	38%	15%	26%
1	2%	4%	6%	10%	8%	18%
Total nests	479	713	132	21	102	102

^a The expected figures are calculated by scaling the initial brood size distributions reported in this study by the inverse hatching success factors appearing in Ross-Smith *et al.* (2015). The abbreviation V-P-S denotes the work of Vermeer *et al.* (1988).

TABLE 4
Average clutch sizes from studies of *L. glaucescens* in the Salish Sea, ordered chronologically^a

Location (Source)	Study year	Number of nests observed	Average clutch size
Mandarte Is. (Vermeer 1963)	1962	479	2.82
Mandarte Is. (Verbeek 1986)	1979	297	2.69
Mandarte Is. (Verbeek 1986)	1980	417	2.77
Protection Is. (Reid 1988)	1984	704	2.73
Vancouver colony (Vermeer <i>et al.</i> 1988)	1986	80	2.70
Vancouver dispersed (Vermeer <i>et al.</i> 1988)	1986	52	2.77
Victoria (Hooper 1988)	1986	22	2.59
Mandarte Is. (Blight 2011, 2012)	2008	210	2.42
Mandarte Is. (Blight 2011, 2012)	2009	175	2.25
Vancouver (observed)	2015	21	2.43
Vancouver (adj. scaled)	2015	102	2.69*
Vancouver (raw scaled)	2015	102	2.39*

^a The average clutch sizes for both the raw and left-censored adjusted data of this study are calculated using the same scalings from Table 3. Here, the asterisks are used to emphasize that these estimates are derived using the post-hoc hatching success scaling factors of Ross-Smith *et al.* (2015).

skewed over time, as one-egg clutches become less rare. This seems to indicate that while urban-nesting Glaucous-winged Gulls may experience higher levels of post-hatch fledging success than their non-urban conspecifics, they are not immune to the environmental factors driving the decline of average clutch size in the greater Salish Sea population.

For further comparison, the average clutch sizes of *L. glaucescens* across all major study sites from the Salish Sea are displayed in Table 4. As noted by Blight (2011), average clutch size exhibits a significant downward trend over time. Using this study’s observed

TABLE 5
Historical temperature and precipitation data with corresponding post-hatch fledging success figures from Hooper (1988), Vermeer *et al.* (1988), Blight (personal communication), and the current study^a

Location	Study year	Daily max temp. July (°C)	Daily min temp. July (°C)	Daily avg. temp. July (°C)	Total July precip. (mm)	Post-hatch fledging success
Victoria	1986	18	10.7	14.4	8.2	71%
Vancouver	1986	19.9	12.8	16.4	62.2	73%
Mandarte Is.	2008	20.6	11.5	16.1	9.6	69%
Mandarte Is.	2009	24.2	14.3	19.3	17.4	64%
Vancouver	2015	25.0	15.6	20.3	33.4	≥ 85%

^a Data were taken from publicly available Government of Canada, Environment and Natural Resources databases. Only post-1985 data were available. Victoria data were recorded at the Gonzales Heights weather station, Vancouver data were recorded at the Coal Harbour station, and Mandarte Island data were recorded at the Saturna Island station.

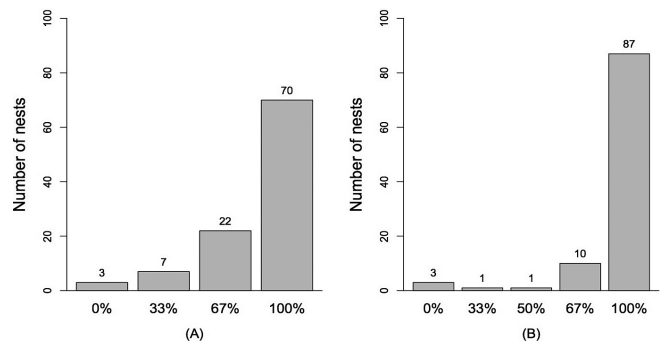


Fig. 3. (A) Post-hatch fledging success rates, adjusted for left-censoring and aggregated over all observation sites. These figures represent the worst-case estimates for post-hatch fledging success. (B) Observed post-hatch fledging success rates, aggregated over all observation sites. No adjustment for left-censoring has been made.

sample estimate, the standard Spearman rank-correlation of time with average clutch size is decisively negative: $\rho = -0.78$ ($P < 0.01$).

Post-hatch fledging success and implications for the regional population

Evidence indicates that urban-nesting Glaucous-winged Gulls in the downtown core of Vancouver exhibit remarkably high levels of post-hatch fledging success. Indeed, even the worst-case figures (i.e., those adjusted for left-censoring) indicate that this breeding subpopulation raises at least 85% of their offspring to fledging, which places their level of post-hatch fledging success among the highest ever recorded for conspecific subpopulations.

Sample estimates from other studies of *L. glaucescens* were derived from one breeding season's data at one breeding location, recorded in each respective row of Figure 4. Broadly speaking, post-hatch fledging success estimates typically fall near one of two levels: 70% or 85% success. It should be remembered that the estimate from the present study appearing in Figure 4 represents the minimum post-hatch fledging success of the study population, as calculated via the adjustment for left-censoring.

Among the 11 studies of subpopulations within the Salish Sea, only the study by Gillett *et al.* (1975) on Colville Island, San Juan Islands, WA, produced estimates of post-hatch fledging success that were of similar magnitude to those in this study. The most recent estimates of Blight (2012), made from the Mandarte Island subpopulation, are significantly lower than the Vancouver estimate reported here. There are only two other studies of urban-nesting populations (Hooper 1988, Vermeer *et al.* 1988), both of which also reported lower post-hatch fledging success, although with higher levels of associated uncertainty that reflect their lower sample sizes (22 and 52 nests, respectively, compared to 102 for the present study).

It seems highly likely that results are at least partially driven by a year effect; for example, especially hot and dry years often lead to higher chick mortality (Vermeer 1963, Ward 1973, Rock 2005). However, upon examining the available historical temperature and precipitation data for the region (see Table 5), precipitation does not appear to explain any of the variability in records of post-hatch fledging success. Moreover, July temperatures in Vancouver during 2015 were hotter than other site-year combinations, reflecting the general fact that summers in the Salish Sea have been getting steadily warmer over the past 30 years. Thus, it seems unlikely that the high

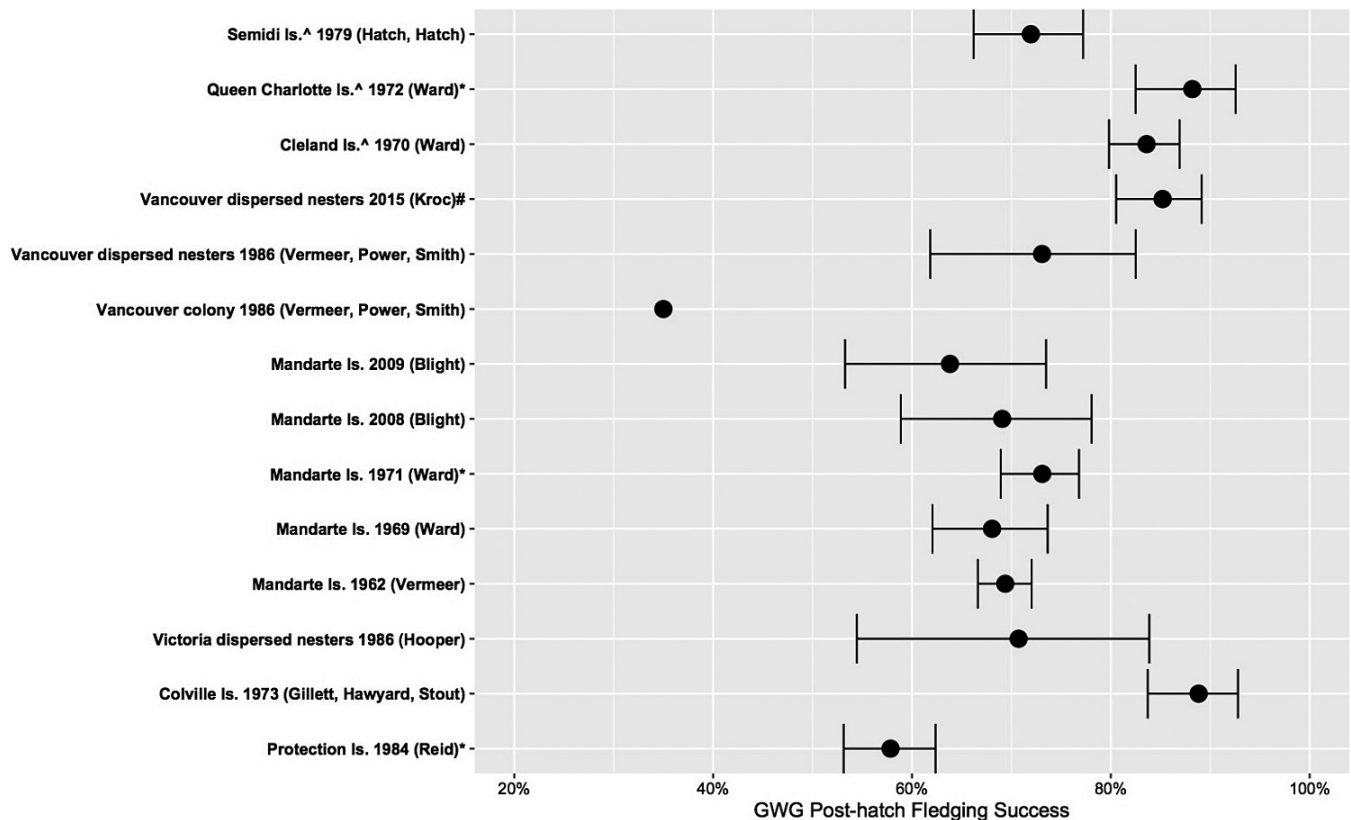


Fig. 4. Observed estimates and associated uncertainties for major studies of Glaucous-winged Gull post-hatch fledging success in various years and at various locations in Washington, British Columbia, and Alaska. Years correspond to the year each study was conducted, not the date of publication. Error bars represent binomial 95% confidence intervals. Estimates have been ordered according to location of study, north to south (top to bottom). Study locations that fall outside the Salish Sea region are indicated by a caret (^). Starred estimates (*) are derived from partial data. The Vancouver colony figure of Vermeer *et al.* (1988) is a census count, so it has no associated confidence interval. A pound symbol (#) marks the figure corresponding to this study, as the minimum post-hatch fledging success estimate is used. From top to bottom, the sources from which these estimates were derived, or in which they appear, are: Hatch & Hatch (1990), Ward (1973), Kroc (current study), Vermeer *et al.* (1988), Blight (pers. comm.), Ward (1973), Vermeer (1963), Hooper (1988), Gillett *et al.* (1975), and Reid (1988).

observed post-hatch fledging success of this study can be attributed to particularly amenable summer temperatures. Assuming no other confounding variables that mediate a study-year effect, results indicate that urban-nesting Glaucous-winged Gulls are producing more fledged offspring per pair than their non-urban counterparts. It is unclear for how long this phenomenon has occurred.

Except for Mandarte Island, post-hatch fledging success has not been recorded in multiple years for a single observation site, and no studies have attempted to record post-hatch fledging success rates for more than one population (e.g., urban vs. non-urban) in a single breeding season. Thus, it is not possible to directly assess possible temporal effects. However, it should be noted that the estimates of Hooper (1988) and Vermeer *et al.* (1988) are consistent with the high level of post-hatch fledging success observed in this study. This may indicate that the high urban post-hatch fledging success rate is somewhat robust to temporal trends. Much work remains to be done to verify this tentative claim.

There are several reasons to expect high post-hatch fledging success rates in urban-breeding gull populations in general, including reduced mortality due to attacks from adult gulls and other native predators. It has been repeatedly shown that attacks from adult gulls are the strongest drivers of mortality rates among unfledged young gulls (Vermeer 1963, Gillett *et al.* 1975, Hunt & Hunt 1975, Kovacs & Ryder 1983). Such attacks are usually precipitated by young chicks mistakenly dispersing into a nearby pair's territory, often in response to a disturbance (Emlen 1956, Harris 1964, Kadlec *et al.* 1969). It should be noted that the methods used in some studies have likely exaggerated these effects, in that researchers often caused these disturbances themselves while collecting data. Regardless, most urban-nesters establish breeding territories on isolated rooftops, which are often small enough to support only a single breeding pair ($\approx 72\%$ according to figures from the present study). This eliminates the possibility of such attacks.

As gulls exhibit a high degree of fidelity toward nesting sites across years and across generations, especially among males (Vermeer 1963, Reid 1988, Rock 2005), a high reproductive success rate relative to non-urban breeding populations has significant implications for the overall distribution and change of the Salish Sea Glaucous-winged Gull population. One may expect to see local populations nesting further inland, nesting more densely in already-established urban-nesting spots, and abandoning historical non-urban-nesting sites in favor of more productive urban ones. This last development may be particularly expected since it has been suggested that Glaucous-winged Gulls will actively immigrate to healthier and more productive colonies (Hatch *et al.* 2011). As each new breeding generation is likely to supply relatively more members from urban-reared backgrounds, any rate of urban colonization could be quite high. Such a shift in breeding location would comply with the findings of Blight *et al.* (2015), who established that the non-urban breeding population has been considerably reduced in the past 35 years. A similar phenomenon has already occurred in the UK and Ireland, where both Lesser Black-backed Gulls and Herring Gulls have emigrated to urban habitats to such an extent that, in some places, they now outnumber non-urban conspecifics by a factor of 4:1 (Rock 2005).

Technical details

The urban study sites of Vermeer *et al.* (1988) were not used for this study, although those authors also studied the reproductive

success of urban-nesters in downtown Vancouver. The urban landscape of the region has changed remarkably since their study was conducted, making direct comparisons across time at fixed locations dubious at best. Moreover, their largest observation site on False Creek was converted from an industrial warehouse district into the residential and low-density commerce community of Olympic Village prior to 2010; virtually no structures remain from the original warehouse district.

The ideal interpretation of all estimates and associated uncertainties presented in this paper assume random sampling from their respective target populations. However, the nature of observational ecology precludes the possibility of satisfying this assumption exactly. Consequently, reported uncertainty estimates should be interpreted conservatively.

The survival of each nestling is not a true Bernoulli trial, since it is not independent of the survival of the chick's siblings. However, any dependence structure that is ignored by treating each survival as a Bernoulli trial is likely to have only a minor effect on the results, as survival rates do not correlate strongly with brood size (Vermeer 1963, Ward 1973). Consequently, the estimates remain reasonable lower bounds.

CONCLUSIONS

Urban-nesting Glaucous-winged Gulls in downtown Vancouver, BC, seem to experience a high level of post-hatch fledging success compared to the success of their non-urban-nesting conspecifics, as indicated in the literature. This differential in post-hatch fledging success could transfer to a similar differential for overall reproductive success between urban and non-urban nesters in the greater Salish Sea region. A better understanding of the population and ecological dynamics between urban and non-urban nesters is crucial for predicting future trends and for assessing the overall health of this important species in an area so heavily impacted by human influence (Halpern *et al.* 2008).

Urban-nesting can surely lead to increased conflict between humans and gulls. In general, nesting gulls can make for noisy neighbors and many species seem remarkably tolerant of human deterrent efforts (Belant *et al.* 1998, Temby 2000, Rock 2005). Humans can also assume a novel destructive role in gull reproduction if eggs and chicks are forcibly removed from nests and either relocated or destroyed. While such actions are prohibited by federal laws in both Canada and the United States, anecdotal evidence indicates that such events are not uncommon (L.K. Blight pers. comm.; M. Phillips [Wildlife Rescue Association of BC] pers. comm.).

Although increased urban-nesting can cause challenges for wildlife management and human cohabitation, it also presents a remarkable opportunity for species conservation. In the case of the Salish Sea Glaucous-winged Gull population, this is especially important to note as non-urban populations have been cut in half over the past 35 years (Sullivan *et al.* 2002, Bower 2009, Blight *et al.* 2015). Simply allowing urban-breeding populations to thrive could be an exceptionally easy way to ensure a healthy and robust population of this critical coastal species.

As traditional, non-urban habitats disappear or degrade due to increased human activity or climate change, the urban environment offers the potential to become an intriguing sanctuary for species

that are amenable to cohabitation with humans. Conservation of breeding habitat is a critical issue in a highly populated and heavily trafficked region like the Salish Sea. Also of concern is the protection of the greater ecosystem's foundational trophic levels, notably the threatened and declining forage fish populations (Therriault *et al.* 2009) on which the highly visible gull populations rely (Davis *et al.* 2015). The potential exists to employ effective conservation strategies that are relatively easy to manage in the urban environment, to better protect and monitor species either at risk or in decline in their traditional habitats.

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