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ABSTRACT

BELLOUT, S., AIT BAAMRANE, M.A. & AOURIR, M. 2022. Breeding parameters of Yellow-legged Gull *Larus michahellis* in the largest Moroccan colony: Natural versus urban nesting sites. *Marine Ornithology* 50: 215–223.

We investigated the main differences in the breeding ecology of Yellow-legged Gulls *Larus michahellis* nesting in urban (city of Essaouira) and natural (Mogador Island) environments on the African Atlantic coast of west-central Morocco during the 2018 and 2019 breeding seasons. This Yellow-legged Gull population is the largest in the southern portion of this species' range, making it excellent for research on the breeding biology of marginal populations. Over two years, we collected data on nest density, chronology, clutch size, egg dimensions, and hatching success from nests across the city and island. Results showed that nest density averaged 1.26 ± 1.03 nests/ha (126 ± 103 nests/km²) in the urban areas and 442 ± 254.56 nests/ha in the natural areas. The laying period was significantly longer at Mogador Island, lasting more than 20 weeks on average and occurring in two egg-laying peaks. Hatching success (number of hatched eggs per nest) in the whole study area averaged $86.04\% \pm 23.01\%$ and was similar between seasons and habitats. Fledging success (number of chicks surviving over 40 days per hatched egg) and breeding success (number of chicks surviving over 40 days per laid egg) in the urban area averaged $54.98\% \pm 23.93\%$ and $46.52\% \pm 22.01\%$, respectively. In both natural and urban habitats, the high hatching success rates, which are the highest values reported among North African colonies, may explain the rapid growth of this population.

Key words: breeding biology, urban birds, Mogador Island, hatching success

INTRODUCTION

The Yellow-legged Gull *Larus michahellis* (hereafter YLG) is one of the most abundant and widely distributed seabirds in the western Mediterranean basin (Olsen 2004, Delany & Scott 2006). Along the Mediterranean coast of Morocco, several colonies occur on the Chafarinas Islands (~4500 breeding pairs; Varela & de Juana 1986), and some small colonies are scattered between the central Strait of Gibraltar and the city of Al Hoceima in Morocco (Cortes & Amezian 2006). On the Atlantic coast of Africa, the Mogador Archipelago (~700 km south of the Strait of Gibraltar, Fig. 1), hosts the largest YLG breeding colony in southern portion of this species' range. The colony population has undergone a sharp increase, from ~500 breeding pairs in 1960 (de Naurois 1961) to 2000–2500 breeding pairs by the 1980s (Beaubrun 1993) to 30 000 birds in 2019 (Bellout *et al.* 2021).

To accommodate the growth, the species has expanded its nesting area to include human-made structures in the nearby urban area of Essaouira, indicating that natural nesting sites of Mogador Archipelago may have become saturated. In fact, while studying the breeding population of Mogador Island using the point transect method in 2019, Bellout *et al.* (2021) recorded a population of almost 5000 pairs, which represents a 250% increase from 1985. Exactly when roof-nesting YLG became established in Essaouira or elsewhere in Morocco is unknown. A number of studies have assessed the reproductive costs and benefits of roof nesting by simultaneously comparing success of gulls on rooftops with those on islands (e.g., Hooper 1988, Belant & Seamans 1993, Annett

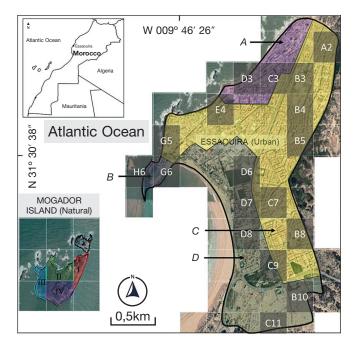


Fig. 1. Location of the two study areas: Mogador Island (Natural) and the city of Essaouira (Urban) on the Atlantic coast of Morocco. The plots sampled for nest density estimation in the different zones of the urban environment (A: Industrial, B: Harbor, C: Residential, and D: Services; denoted by shading) are represented by an alphanumeric code that is separate from the zone designations.

& Pierotti 1999, Perlut *et al.* 2016, Kroc 2018). For example, Dolbeer *et al.* (1990) suggested that buildings are suboptimal nesting habitats, due in part to the quality and availability of food from anthropogenic sources (Monaghan 1979, Belant & Seamans 1993). Hooper (1988), studying a colony of roof-nesting Glaucous-winged Gulls *Larus glaucescens* in British Columbia, Canada, reported that roof-top and island nests had equal hatching success. In contrast, Perlut *et al.* (2016) found that European Herring Gulls *Larus argentatus*, nesting in roof-top colonies had lower hatching success than those nesting on Appledore Island in York County, Maine, USA.

In this paper, we report a comparison of YLG breeding ecology between two areas: natural Mogador Island and urban Essaouira, comparing nesting densities and breeding parameters (i.e., laying date, clutch and egg sizes, and hatching success). Our results provide better understanding of the breeding dynamics of this population, the largest on the West African Atlantic coast, to facilitate more effective management. This is especially relevant if the increase of this urban gull population leads to increased conflicts with Essaouira's human inhabitants.

METHODS

Study area

Essaouira (31°31'N, 009°45'W) is a small city whose boundaries encompass 9000 ha (90 km²). The human population numbers 77966 persons (Royaume du Maroc 2014) but occupies a built area of < 600 ha. The city is divided by the Regional Planning Agency into four main areas (Fig. 1): the Industrial area (41 ha), which consists of factories, workshops, and warehouses; the Harbor area (13 ha), which consists of guays and buildings related to the fishing industry; the Residential area (240 ha), which designates all urban areas where housing is the predominant function of buildings; and the Services area, which is dedicated to services like hotels, banks, and administration (161 ha). The city is located on Morocco's central Atlantic coast. Offshore by 1.2 km is the Mogador Archipelago, which is composed of eight calcareous islands and islets. Mogador Island, where we conducted our study, is the most accessible of these. It is a single landmass at low tide, but at high tide, a small portion is submerged. The two resulting islands are D'zira Ikbira (Big Island), which is 21.9 ha and reaches 29 m above sea level (a.s.l.), and Firaoun (Pharaoh Island), which is 2.1 ha, reaches 26 m a.s.l., and has a crater in the middle. Neither island is inhabited by people and both are fully protected by conservation laws.

The biological reserve of the Mogador Archipelago is home to an important breeding avifauna, and it has been entirely protected since 1980; in 2005 it was classified as a RAMSAR site. The principal vegetation is a mixture of grasses, *Lycium intricatum* (Solanaceae), *Suaeda fruticosa* (Amaranthaceae), and *Mesembryanthemum crystallinum* (Aizoaceae).

Field procedures

Fieldwork was carried out from late January to late July during two consecutive breeding seasons (2018 and 2019) in Essaouira (urban) and on Mogador Island (natural). We established 60 study plots in the study area (54 and 6 in urban and natural locations, respectively) using a 0.36×0.36 km UTM grid.

Nest density estimation

In the urban location, we selected 33% of the plots (n = 18) by random drawing of identification numbers. We searched for nests using a combination of methods, including surveying from vantage points between 08h30 and 17h00. In the selected urban plots, all accessible rooftops with evidence of nesting pairs were prospected, and reachable nests were geographically tagged then visited twice weekly.

After finding a nest in the urban area, the following parameters of the building were recorded: height of roof from ground level, number of stories, type of roof, roofing material, and purpose of the building. Buildings were conditionally divided according to their purpose into the following categories to mirror the city's classification system: Harbor facilities, Residential buildings, Service and administrative buildings, and Industrial structures

 TABLE 1

 Data of plots and quadrats (area and number of counted

 Yellow-legged Gull Larus michahellis nests) and nest densities
 in both urban (Essaouira) and natural (Mogador Island)

 localities during two consecutive breeding seasons
 in both urban (Essaouira)

Plot	Area (ha)	Quadrat	Nests per quadrat		Nests per plot		Nest density (/ha)	
			2018	2019	2018	2019	2018	2019
Essao	uira							
D3	6.40	_	-	-	7	9	1.09	1.41
C3	8.93	-	-	-	26	29	2.91	3.25
A2	11.01	-	-	-	19	15	1.73	1.36
B3	13.55	-	-	-	15	11	1.11	0.81
B4	13.55	-	-	-	14	12	1.03	0.89
E4	9.33	-	-	-	9	13	0.96	1.39
B5	10.46	-	-	-	17	14	1.63	1.34
G5	6.25	-	-	-	13	14	2.08	2.24
D7	2.77	-	-	-	13	9	4.69	3.25
B8	4.55	-	-	-	4	7	0.88	1.54
G6	7.41	-	-	-	15	11	2.02	1.48
H6	3.72	-	-	-	3	4	0.81	1.08
D6	10.45	-	-	-	1	1	0.10	0.10
D7	10.81	-	-	-	8	9	0.74	0.83
E7	5.11	-	-	-	1	2	0.20	0.39
C9	13.55	-	-	-	2	1	0.15	0.07
B10	2.28	-	-	-	2	2	0.88	0.88
C11	11.90	-	-	-	1	1	0.08	0.08
Moga	dor Isla	nd						
I	4.06	Q1	52	45	3380	2925	832	720
II	6.76	Q2	12	9	1298	973	192	144
III	3.42	Q3	21	15	1149	821	336	240
IV	7.73	Q4	31	36	3832	4450	496	576

(workshops and factories). The number of nests per occupied roof was determined; here, the term roof refers to "a single contiguous surface covering one or more buildings" (Blight *et al.* 2019). Nest density was calculated using two methods. The first method was the number of nests per unit of plot area. This plot area was corrected for the peripheral plots, which included non-urban parts (i.e., the area we considered excluded non-urban features). The second method was the number of nests per unit of zone area (Industrial, Residential, Harbor and Services).

On Mogador Island, we defined four zones (I, II, III, and IV; Fig. 1) depending on the exposure to the prevailing winds (i.e., winds with northern and southern components), but wind direction was not considered in the final analysis. In each of the four zones, we set up a 25×25 m quadrat (Q1, Q2, Q3, and Q4) during early April of each breeding season to estimate the nest density within each zone. Each quadrat was surveyed twice within an interval of 5–7 days. The mean number of nests counted among the quadrats was used to estimate density in each zone.

Breeding parameters

Of all detected nests in the two habitat types, a subset of permanently accessible nests in Essaouira (i.e., nests whose accessibility is authorized by the owner of the structure) and a subset of nests on Mogador Island (randomly selected so as to cover all of the island's microhabitats) were considered for the breeding biology survey. During the field inspection, nests were marked with small coded flags and their exact locations were recorded with a GPS device (Garmin eTrex 20x).

Laying date was determined by direct observation of the first egg laid or by back-calculation from the hatching date (incubation period is 28 days; Beaubrun 1988). The frequency of nest initiation (also known as the "clutch frequency") is defined as the number of nests initiated every 10 days from February 01. A nest was considered active when it contained at least one egg, and it was considered abandoned when eggs remained for 40 days without hatching. Using an indelible and non-toxic ink marker, eggs and their laying order were marked with letters (A, B, and C). When all eggs were laid and the clutch was completed, we recorded the clutch size and used a digital caliper to measure the width and length of each egg to the nearest 0.1 mm. Clutch size was recorded only if it remained constant between two visits, so our observations did not account for eggs lost due to predation prior to the first visit or during egg-laying. Egg volume was calculated following Harris (1964), according to

$$V = \frac{l \times w^2 \times k}{1000}$$

where V is egg volume (mm^3) , l is egg length (mm), w is egg width (mm), and k is the constant 0.476.

The incubation period was defined as the time between the first egg being laid and the first egg hatching. The hatching date of the first egg was determined with an accuracy of ± 1 day. Mean hatching success (number of hatched eggs per nest) was calculated for both locations. Fledging success (number of chicks surviving over 40 days per hatched egg) and breeding success (number of chicks surviving over 40 days per laid egg) were defined exclusively in the urban area, as it was difficult to monitor hatched chicks emanating from each surveyed nest on Mogador Island to evaluate fledging and overall breeding success. This was due to high nest density and synchronous hatching of chicks; tracking chicks would have resulted in too much disturbance because the chicks could not be precisely assigned to their nests.

Data analysis

The reproductive parameters we compared between habitats were nest density, egg-laying chronology, clutch size, egg dimensions/ volume, and hatching success. We used parametric tests unless the data distributions violated the assumptions of homoscedasticity (equality of variances) and normality of distributions (Kolmogorov-Smirnov test) when equivalent nonparametric tests (Mann-Whitney U test) were used. We used a parametric *t*-test when variances were equal or Welch's *t*-test when variances were unequal, in addition to analysis of variance (ANOVA). Post-hoc comparison was made using the Tukey test. Chi-squared tests were used for comparisons involving frequency data, such as hatching success (proportion of hatched nests among the monitored nest sample). All statistical tests were carried out using SPSS v.21 (SPSS; Chicago, USA). Differences were considered statistically significant at P < 0.05.

For analysis of nest density, sample size in the urban environment was the number of georeferenced nests (n = 334 nests). For breeding parameters, we used a subsample of these nests to assess breeding chronology (n = 125), as well as clutch size and hatching success (n = 67). For nests in the natural location, the sample size to establish breeding chronology was n = 533 nests of which 81 were used to evaluate clutch size and hatching success. Egg biometry was obtained from a sample size of 180 and 227 eggs for the urban and natural locations, respectively.

Over the entire study period, we geotagged 334 active nests in the urban environment (i.e., 170 and 164 nests in 2018 and 2019, respectively).

RESULTS

Nest site, characteristics, and densities

Roof-nesting YLG typically nest on flat concrete roofs, close to any structure that can provide shade (such as walls, solar panels, or any larger objects), in areas that are obstructed from view. Overall, 90% of nests included in our study were located on buildings with heights of 2–15 m; the industrial flour mill was the highest building housing nests in the entire urban area. The remaining 10% were found at ground level in backyards and in unbuilt lands of the city. Depending on the purpose of the building, we noted that private, public, and industrial facilities host YLG nests equitably (34.43%, 31.44%, and 27.25%, respectively), with hotels and commercial buildings hosting only 6.88% of urban nests.

The spatial distribution of the urban nests showed great heterogeneity. The mean nest density (Table 1) did not show any significant difference between years: 1.28 ± 1.14 nests/ha in 2018 and 1.24 ± 0.93 nests/ha in 2019, with an average of 1.26 ± 1.03 nests/ha for both years (t = 0.126, df = 34, and P = 0.901). The mean density per urban zone was also heterogeneous and ranged from 0.37 ± 0.35 to 2.16 ± 1.07 nests/ha (ANOVA: $F_{3.32} = 5.415$, P = 0.004). The Tukey test revealed significant differences between

nest density in the Services area $[0.37 \pm 0.35 \text{ nests/ha}]$ compared to the Residential area $[1.68 \pm 1.02 \text{ nests/ha}, P = 0.015]$ and Industrial area $[2.16 \pm 1.07 \text{ nests/ha}, P = 0.009]$.

The GPS locations of urban nests indicated that 42.4% of 2018's nests were re-used during the 2019 breeding season. The Industrial area showed the greatest re-use rate with more than 51.5% (17/33), followed by the Residential area (46.2%), and then the Services area and Harbor area with 26.6% and 11.1%, respectively.

On Mogador Island, YLG occupied territories year round and started laying eggs in late February to early March. Available nesting habitat ranged from open, densely vegetated flat areas to rocky sites with no vegetation. Nest density in this saturated natural environment averaged 464 ± 274.96 nests/ha in 2018 and 420 ± 272.59 nests/ha in 2019 (Table 1). An average annual breeding population of 9709 breeding pairs at the first nesting peak was recorded in the first half of April. This is more accurate than the point transects referenced above.

Breeding chronology and laying frequency

Overall, we recorded the nest initiation date for 232 nests in 2018 and 426 in 2019. Over two years, the first egg-laying dates were noted for 125 and 533 nests through the breeding period (from first egg to last fledging) in urban and natural sites, respectively. For all nests, the distributions of laying dates differed from normal (Kolmogorov-Smirnov test: Z = 0.180, n = 125, P < 0.001 for urban nests; Z = 0.194, n = 533, P < 0.001 for natural nests). The earliest eggs were found on Mogador Island on 11 February 2018 and 20 February in 2019, with laying extending to mid-July (04 July 2018 and 13 July 2019, see Figs. 2, 3). In Essaouira, the first eggs were recorded on 18 March 2018 and 09 March 2019, and the last eggs were laid on 29 May 2018 and 16 June 2019. The natural YLG population exhibited an extended mean laying period of > 20 weeks vs. 12 weeks for the urban population but without significant differences. Mean laying dates ± standard error, expressed as number of days from 01 February, were 83.80 ± 1.61 days for urban nests (*n* = 125) and 83.05 ± 1.53 days for the natural nests (n = 533); Welch's *t*-test: $t'_{656} = 0.115$, P = 0.735). Clutches were initiated in the natural location 20 days earlier than in the urban area (Figs. 2, 3).

The difference in clutch frequencies during the whole study period is highly significant between the two habitats (Mann-Whitney U = 27393, Z = -3.116, P = 0.002). This revealed two egg-laying

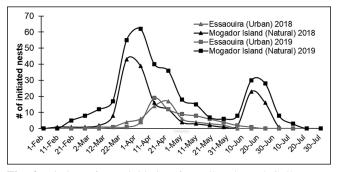


Fig. 2. Timing of nest initiation for Yellow-legged Gulls *Larus michahellis* in Essaouira, Morocco, (Urban) and on Mogador Island (Natural) during the 2018 and 2019 breeding periods.

peaks on Mogador Island, the first in mid-April (second and third weeks) and a second smaller peak during late June into the first week of July. In the urban habitat, only one egg-laying peak was observed from late-April to mid-May (Fig. 2).

Clutch size

Not all measures were obtained for all nests, due to the occasional lack of accessibility in the urban area, where nests could be seen but not necessarily reached. The modal clutch size in both habitats was 3 eggs through the study period, with a non-normal distribution (Kolmogorov-Smirnov test: Z = 0.445, n = 67, P < 0.001 for urban clutches; Z = 0.492, n = 81, P < 0.001 for natural clutches). On Mogador Island, mean ± standard deviation (SD) clutch size was 2.86 ± 0.35 eggs per nest (n = 51) in 2018 and 2.70 ± 0.53 eggs per nest (n = 30) in 2019 (Table 2). The difference between the years was not significant (Mann-Whitney U = 662.5, Z = -1.488, P = 0.137). On the other hand, YLG nesting on rooftops and other urban habitats in Essaouira exhibited a mean $(\pm SD)$ clutch size of 2.78 ± 0.42 eggs per nest (n = 32) in 2018 and 2.60 ± 0.65 eggs per nest (n = 35) in 2019, without significant variation among years (Mann-Whitney U = 496, Z = -1.039, P = 0.299). Since we did not detect any significant differences in clutch size between the two years, we pooled the data to look for possible differences depending on habitat. Once again, the Mann-Whitney U test did not reveal any significant difference between habitats (Mann-Whitney U = 2473.5, Z = -1.278, P = 0.201). Therefore, pooling data for the whole region gives a global mean clutch size of 2.75 ± 0.49 (n = 148) eggs per nest.

Egg measurements and laying order

The distributions of egg volume (Table 2) did not differ from normal (Kolmogorov-Smirnov test: Z = 0.060, n = 180, P = 0.2 for urban eggs; Z = 0.054, n = 227, P = 0.2 for natural eggs).

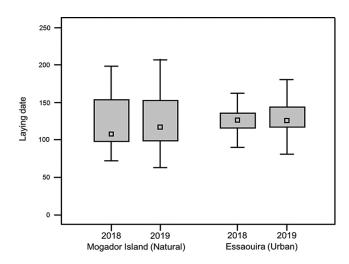


Fig. 3. Laying dates at Yellow-legged Gull *Larus michahellis* colonies in Essaouira, Morocco, (Urban) and on Mogador Island (Natural). The y-axis shows the laying date as the number of days from the start of the breeding season (01 January by convention). The whiskers represent the min and max values. The box contains the values between the first quartile and the third quartile, and the square represents the median value.

Clutch size and biometrics of Yellow-legged Gull Larus michahellis eggs in Essaouira and on Mogador Island, Morocco ^a										
	Breeding location and season									
Egg measurements	Essaouira (Urban)				Mogador Island (Natural)					
	2018	2019	Total	Р	2018	2019	Total	Р		
Clutch size	2.78 ± 0.42 [32]	2.60 ± 0.65 [35]	2.69 ± 0.56 [67]	0.299*	2.86 ± 0.35 [51]	2.70 ± 0.53 [30]	2.80 ± 0.43 [81]	0.137*		
Length (mm)	69.65 ± 3.27	70.63 ± 2.63	70.14 ± 3.00	0.028	70.69 ± 3.14	71.16 ± 2.52	70.86 ± 2.93	0.220		
Width (mm)	47.21 ± 1.49	46.46 ± 1.35	46.83 ± 1.47	0.001*	47.84 ± 1.71	47.72 ± 1.42	47.80 ± 1.61	0.333*		
Volume (mm ³)	74.08 ± 7.06	72.69 ± 5.75	73.38 ± 6.45	0.151	77.16 ± 7.03	77.22 ± 5.69	77.18 ± 6.57	0.953		

[180]

 TABLE 2

 ch size and biometrics of Yellow-legged Gull Larus michahellis eggs in Essaouira and on Mogador Island, Morocco

^a Sample size: mean ± SD [sample size], *P*: significance of *t*-test.

[91]

[89]

* Mann-Whitney U test was used

No significant difference was found between years (Fig. 4) for egg volumes on either Mogador Island (mean egg volume = 77.18 ± 6.57 mm³, n = 227; t = -0.059, P = 0.953) or Essaouira (mean egg volume = 73.38 ± 6.45 mm³, n = 180; t = 1.443, P = 0.151). Urban areas exhibited significantly lower egg volumes than natural areas (t = 5.853, P < 0.001), and egg dimensions were significantly different between years (Table 2) in Essaouira (length and width). As expected, based on egg size by laying order in other gulls (Pons 1993, Kilpi *et al.* 1996, Bosch *et al.* 2000, Soldatini *et al.* 2008), laying order had a significant effect on egg volume, with the first egg (A) being larger than the second (B), which was larger than the third (C) (ANOVA: $F_{2.404} = 82.04$, P < 0.001).

Eggs laid in sequence exhibited a volume loss between the A and B eggs, then between the B and C eggs of $5.40\% \pm 4.55\%$ and $6.55\% \pm 5.60\%$, respectively, on Mogador Island and $6.88\% \pm 4.46\%$ and $6.25\% \pm 4.48\%$ in Essaouira. This volume loss was significantly different only between eggs A and B (ANOVA: $F_{1.113} = 4.375$, P = 0.039).

Incubation period

No differences existed in the length of the incubation period between years $(28.73 \pm 1.02 \text{ days in } 2018 \text{ vs. } 29.07 \pm 0.98 \text{ days in } 2019 \text{ on Mogador Island; } 28.37 \pm 0.93 \text{ days in } 2018 \text{ vs. } 28.45 \pm 0.62 \text{ days in } 2019 \text{ in Essaouira})$, unless taking habitat type into account (t = 2.850, P = 0.005). The length of the incubation period was estimated in the natural habitat at $28.85 \pm 1.01 \text{ days}$, compared to $28.41 \pm 0.78 \text{ days}$ in the urban habitat.

Breeding performance

Hatching success was assessed for 227 eggs on Mogador Island and for 180 eggs in Essaouira. Overall, Mogador hatching success (90.54% ± 15.11%) was not significantly different ($\chi^2 = 11.59$, df = 3, P = 0.157) from the urban area (80.60% ± 29.10%) between the two breeding seasons. Fledging success, breeding success, and chick productivity in the urban area averaged 54.98% ± 23.93%, 46.52% ± 22.01%, and 1.24% ± 0.61%, respectively (Table 3).

DISCUSSION

[146]

Yellow-legged Gull is among those larids that exhibit great plasticity and adaptability in their foraging strategy, making the species a good model to assess the differences in nesting between natural and urban habitats. For this purpose, data were collected at two colonies (Essaouira and Mogador Island) that were located in the same geographic area. Based on a recent survey, these adjacent colonies represent the largest North African YLG population, estimated at 30 000 birds in 2019 (Bellout *et al.* 2021). The large increase in population size during recent decades has likely led to the colonization of the urban environment in order to compensate for the saturation of "natural" habitat. Our surveys showed high nest density (i.e., high competition for nest sites) at Mogador Island and lower nest densities in Essaouira, mostly in the Services and

[81]

[227]

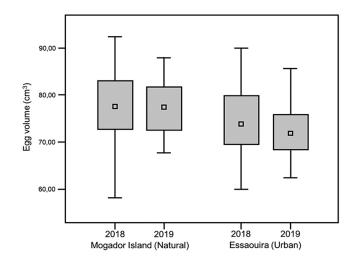


Fig. 4. Inter-annual comparison of Yellow-legged Gull *Larus michahellis* egg volume between Moroccan colonies at Mogador Island (Natural) vs. Essaouira (Urban) and between years (2018 vs. 2019). The whiskers represent the min and max values. The box contains the values between the first quartile and the third quartile, and the square represents the median value.

Duradina	This	Beaubrun (1988)	
Breeding performance indicator	Essaouira Mean ± SD [67]	Mogador Island Mean ± SD [81]	Mogador Island Mean ± SD
Hatching success (%)	80.60 ± 29.10	90.53 ± 15.12	87.17ª
Fledging success (%)	54.98 ± 23.93	-	79.65 ^a
Breeding success (%)	46.52 ± 22.01	-	77.94 ± 3.53^{b}
Chick productivity	1.24 ± 0.61	-	1.28 ± 0.06^{b}

TABLE 3
Breeding performance of the Yellow-legged Gull Larus michahellis in Essaouira and on Mogador Island, Morocco

^a Standard deviation (SD) unavailable

^b Averaged from three years of survey (1978, 1980, and 1983)

Harbor areas. Within the urban landscape, the highest density was in the Industrial area. This distribution may depend on two main factors: the availability of favorable nesting sites and the presence of accessible food resources. Regarding nesting sites, Essaouira's YLGs prefer prominent buildings (ground floor plus more than two stories), whose terraces or roofs are rarely visited by people or pets (Derradji & Moulaï 2020). In this sense, the Industrial area constitutes an adequate refuge for nesting because the majority of buildings currently remain abandoned after a glorious industrial past (1970s-2000s). As for food availability, we noticed that nesting density is higher in the areas where anthropogenic waste production is elevated and where urban waste management is inadequate. This happens in the Residential area, which is characterized by uncontrolled deposits of waste and where the garbage bins are in poor condition or almost absent. The Industrial area showed the greater nest re-use rate (52%), followed by the Residential area (46.4%), enhanced by nest site availability on abandoned industrial hangars and buildings. All have tiled roofs, which makes them inaccessible to people and predators. Generally, roofs are flat except for some sloped ones in the Industrial area. The choice of nest sites in urban areas is likely to be influenced by human accessibility to the nest, predators, and microclimate (Parsons & Chao 1983). As for the Industrial area, which has the highest nest density, the presence of a large number of abandoned and inaccessible industrial sheds may be the main reason for this choice by gulls.

As was documented elsewhere in North Africa, YLGs start laying at the end of winter, in the first week of March (Beaubrun 1988; Moulaï *et al.* 2005, 2006; Bougaham & Moulaï 2013; Baaloudj *et al.* 2014, Talmat-Chaouchi *et al.* 2020). The laying initiation dates recorded in this study (i.e., 11 February 2018 and 20 February 2019) are among the earliest reported to date; the earliest is 12 January at the Oued Charef dam in northeastern Algeria (Boukrouma *et al.* 2021). This trend toward earlier egg-laying dates may be a response to breeding density with a steeper slope at higher densities, as documented in other bird species (Bourret & Garant 2015). Indeed, the continual increase in the size of the YLG breeding population has led to a lengthening of the egglaying period (~143 days currently vs. 40 days in the 1980s, Beaubrun 1988), in addition to colonizing the urban environment.

The timing of nest initiation showed two peaks on Mogador Island and only one in Essaouira, which occurs just after the first peak on Mogador Island. This might well be explained by the saturation of nesting sites in the natural environment, such that unoccupied nesting sites are becoming more rare. The second peak of nesting activity at Mogador was likely related to the earlier onset of nesting, which would allow second clutches or successive breeding attempts in case of failures.

Mean clutch size recorded in Essaouira $(2.69 \pm 0.56 \text{ eggs/nest})$ was slightly lower but not significantly different than that recorded on Mogador Island (2.80 ± 0.43 eggs/nest). This is in accord with previous studies (Perlut et al. 2016, Bailly et al. 2017), which showed that clutch sizes are generally smaller for urban colonies. One exception to this tendency has been observed in downtown Vancouver (Canada), where urban-nesting Glaucous-winged Gulls appear to have higher post-hatch fledging success than non-urbannesting conspecifics (Kroc 2018). For natural colonies, the mean clutch size in the present study was higher than that recorded by Beaubrun (1988) for the Mogador population (2.47 eggs/nest) and those documented on the Chafarinas Islands in Northern Morocco (2.69: Vaerla & De Juana 1986) and elsewhere in Algeria (2.7: Jacob & Courbet 1980; 1.4-2.6: Moulaï et al. 2006; 2.13: Talmat-Chaouchi et al. 2020). Mogador clutch size was within the range documented in colonies along the northern shore of the Mediterranean Sea (2.6-2.9: Borgo et al. 1991, Oro et al. 1995, Bosch & Sol 1998, Bosch et al. 2000, Duhem et al. 2002).

On Mogador Island, mean egg volumes were identical to those measured in the same area by Beaubrun (1988) and significantly larger than in Essaouira (77.18 \pm 6.57 vs. 73.38 \pm 6.45 mm³). Since both natural and urban breeders have the same access to urban food resources (because both colonies are adjacent and located in the same geographic area), these changes in egg volume cannot be linked to low-quality food items in urban area. Therefore, we suggest that the Mogador Island colony is composed predominantly of older, experienced breeding females that are more efficient at food acquisition and foraging, which allows them to lay larger eggs. By contrast, younger females nesting in Essaouira have less experience in the acquisition of high quality food (Christians 2002). Moreover, their oviducts may not yet be fully developed and thus produce smaller eggs (Robertson et al. 1994, Forslund & Pärt 1995, González-Solís et al. 2004). Therefore, we propose that the urban-nesting colony in Essaouira is composed mostly by young and less experienced pairs excluded by the severe competition at the natural nesting site. Reinforcing this assumption might be the inter-annual instability observed in egg dimensions in the urban environment, indicating underperforming birds. In addition, younger gulls typically start laying later than older ones, and they lay smaller eggs and/or clutches (Ryder 1975, Haymes & Blokpoel 1980, Ryder 1980, Nisbet *et al.* 1984).

The incubation period of eggs by gulls nesting in the urban environment was shorter than in the natural environment. We propose two hypotheses, which are neither completely contradictory nor exclusive, to explain this difference in egg incubation efficiency observed between urban and natural environments. Our first hypothesis is related to gulls leaving nests in search of food to meet their energy needs. Urban food resources are easily available and more predictable in both space and time (Marzluff 2001, Shochat 2004, Spelt et al. 2019), whereas in the natural environment, food resources (e.g., arthropods) are accessible at irregular periods when local meteorological conditions (e.g., moist or wet ground) promote their availability (Sibly & McCleery 1983, Buckley & McCarthy 1994, Coulson & Coulson 2008). In general, anthropogenic food resources are closer to urban nests. A shorter distance from the nest would imply less travel time and thus shorter, more frequent, and more efficient foraging trips with higher net energy intake (Hunt 1972). According to this hypothesis, the gulls nesting on Mogador Island will take longer to seek their natural and/or anthropogenic food by travelling a minimum of 1.2 km (the distance that separates Mogador Island from Essaouira) further than gulls nesting in Essaouira. For our second hypothesis to explain differences in egg incubation efficiency, we have demonstrated a significant difference in the egg volume between urban and natural environments, with larger eggs on Mogador Island. This could explain the difference in the incubation period, as was demonstrated for European Herring Gull, where a 17 cm³ difference in egg volume should result in a 25-hour difference in incubation period due to egg size alone (Parsons 1972).

In both natural and urban habitats, hatching success (90.53% and 86.04%, respectively) was equivalent to the highest values reported in North African colonies (75.9%: Varela & de Juana 1986; 23%–88.5%: Moulaï *et al.* 2006; 67%–77%: Baaloudj *et al.* 2014; 79.2%: Boukrouma *et al.* 2021). However, it was slightly lower than that of European colonies of this species (94.7%–97.4%: Oro *et al.* 1995; 91.5%–94.5%: Bosch *et al.* 2000; 96.9%: Skórka *et al.* 2005).

Essaouira is attractive to gulls due to the amount of food available, as the majority of street garbage cans are in poor state and uncovered, in addition to the presence of a fish market that produces a very large quantity of fish waste. That market is placed directly in the open air, so it is accessible to scavengers. Nesting in the urban environment appears to be an alternative to competing for saturated natural habitat; YLG are finding high hatching success on rooftops, where space is available and both predation risk and human disturbance are low. Contributing to this success is the availability of abundant and stable food sources year round. Therefore, we hypothesize that the urbannesting colony in Essaouira will continue to grow during the coming decades, with continued saturation of Mogador Island. This might change if anthropogenic waste management measures are undertaken more seriously. Indeed, the closure of open dumps in favor of a technical landfill center and good waste management could reverse the increase in YLG numbers (Bellout et al. 2021) and their colonization of the urban environment, a

pattern observed elsewhere (Galarza 2015, Zorrozua *et al.* 2020, Birouk & Moulaï 2021).

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