J. Field Ornithol., 57(1):22–33

ASPECTS OF THE BREEDING BIOLOGY OF AN EXPANDED POPULATION OF GLAUCOUS-WINGED GULLS IN BRITISH COLUMBIA

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Food supply influences clutch size (Coulson and Horobin 1976, Hussell 1972), laying interval (O'Connor 1979), and egg size and weight (Evans and McNicholl 1972, Pierotti 1982, Verbeek 1970). In British Columbia the Glaucous-winged Gull (*Larus glaucescens*) has increased about 3.5 times in numbers in the last 50 years (Campbell 1975, Drent and Guiguet 1961) and nearly doubled in the Straits of Georgia and Juan de Fuca between 1960 and 1974 (Campbell 1975). Other species of gulls have also increased in numbers (Connover 1983, Harris 1970, Verbeek 1977). Given this increase in numbers of Glaucous-winged Gulls in British Columbia one would expect changes in the various reproductive parameters, including those mentioned.

The reproductive biology of the Glaucous-winged Gull on Mandarte Island, Georgia Strait, British Columbia, has been studied previously in 1961 and 1962 (Vermeer 1963). I use Vermeer's (1963) data base to compare the reproductive parameters he obtained with similar data obtained 18 years later. In addition, I provide information on several parameters not dealt with by Vermeer (1963) that may be useful in future comparisons of reproductive performance, especially now that a plant will be built to incinerate garbage from the Greater Vancouver Regional District (Anonymous 1985, Eberts 1985).

STUDY AREA AND METHODS

Data were collected on Mandarte Island in Georgia Strait, British Columbia. The gulls on the island nest in grassy meadows surrounded by shrubs. The meadows in which I did my research are marked on Fig. 1, and all of them, except number 11, were used by Vermeer (1963). My assistants and I lived on the island from late April to late July in 1976–1980. The meadows were searched in 1979–1980 for new eggs once per day in the morning, as much as possible at the same time. Each nest was marked with a numbered stake and each egg was numbered in India ink, so that for each nest we knew the order and day in which the eggs were laid. Eggs were measured in mm with vernier calipers to 2 decimal places, and they were weighed to the nearest 0.5 g in the field with a Pesola balance on the day they were laid. The hatching of each egg was followed until the young had fully emerged from the egg. Thus a daily record was obtained for each egg from when it was laid until the chick emerged. Only first clutches were considered.

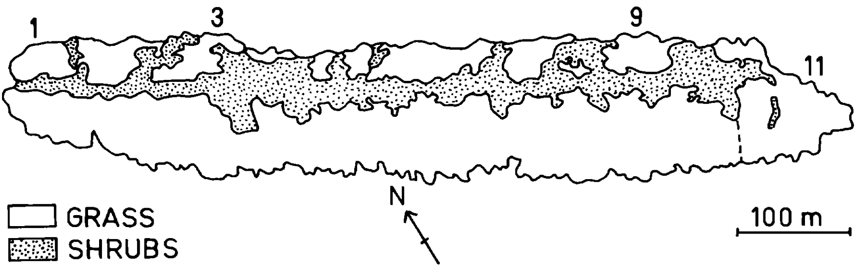

FIGURE 1. Mandarte Island. The numbers indicate the gull meadows in which I did my research.

RESULTS

Nest density.—In 1980 we measured the nearest neighbor distance of 247 nests in 4 gull meadows (Fig. 1). Territory size appeared to be related to openness of the habitat, as was found by Haycock and Threlfall (1975) and Burger and Lesser (1980) for Herring Gulls (*L. argentatus*). The smallest mean internest distance (1.74 ± 0.73 m, n = 50) occurred on meadow 1, which consisted mostly of flat rocks, bare soil, and very little grass. In contrast, gull meadows 3 and 9 consisted of areas of short or tall grass with a few scattered flat rocks. On these two meadows the mean internest distance was 3.09 ± 1.27 m (n = 67) and 3.18 ± 1.46 m (n = 55), respectively. Meadow 11 was intermediate in characteristics and had a mean internest distance of 2.46 ± 0.87 m (n = 75). The overall mean internest distance was 2.64 ± 1.24 m (n = 247).

Timing of egg laying.—The median date of laying ranged from 28 May to 5 June (Fig. 2). Similar annual consistency has been reported for other species of gulls (Davis 1975, Montevecchi et al. 1979). In 1976 the median date of laying of first eggs occurred early. A similar pattern developed in 1980, but apparently because of exceptional bad weather in the last 10 d of May, few clutches were started in that period, so that the median date of laying fell in June.

Clutch size.—The distributions of clutch sizes in 1979 and 1980 did not differ significantly from each other and were lumped (28 clutches of 1 egg, 131 of 2 eggs, 554 of 3 eggs, and 1 of 4 eggs). The mean clutch size in 1979 (2.69 ± 0.59 eggs/nest, n = 297) was not significantly different (Wilcoxon 2-sample test, $P > 0.05$) from that in 1980 (2.77 ± 0.47 eggs/nest, n = 417). The mean clutch size on meadow 1, and on meadow 3 and 9 combined (Fig. 1), was 2.84 (n = 117) and 2.79 (n = 177) eggs/nest, respectively.

In both years, early nests (egg laying started on or before the median date of all first eggs) had a significantly (χ^2 test, $P < 0.001$) larger mean clutch size than late nests (Table 1). This has been reported for other gulls (Davis 1975, Mills 1979, Parsons 1972).

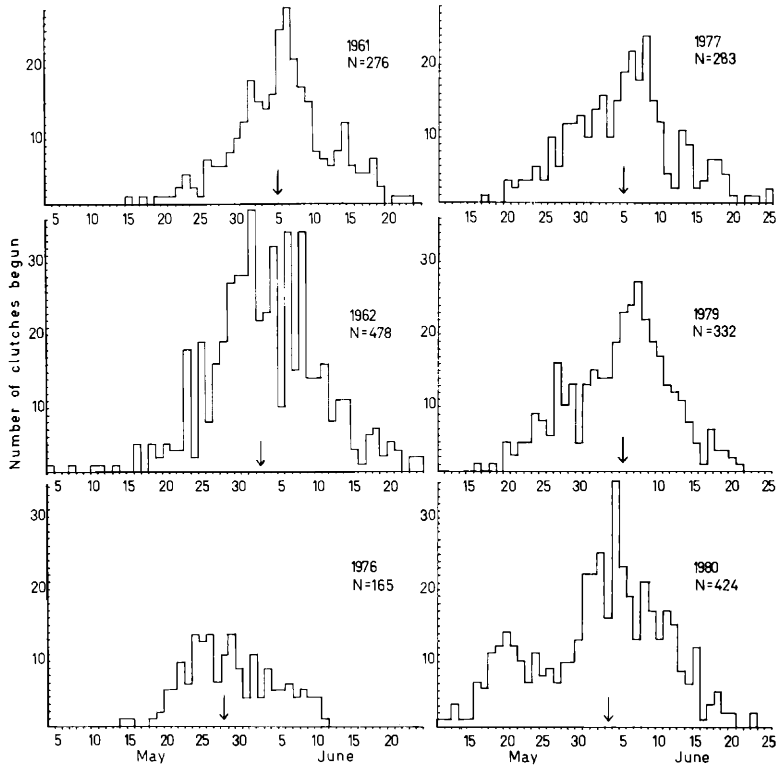

FIGURE 2. Time distribution of first eggs in nests of Glaucous-winged Gulls on Mandarte Island. Arrows indicate the median date of first eggs. Data for 1961 and 1962 are from Vermeer (1963).

Egg weight.—Mean egg weights for *a* (the first egg laid in a clutch), *b,* and *c* eggs are shown in Table 2. In 3-egg clutches, *c* eggs were significantly ($P < 0.001$) lighter in both years than *a* and *b* eggs, while *a* and *b* eggs did not differ significantly from each other in weight. Similar

TABLE 1. Clutch size of Glaucous-winged Gulls early and late in the egg-laying season (1979 and 1980).

Clutch size	Early nests[a]		Late nests	
	n	%	*n*	%
1	2	0.6	26	8.3
2	40	11.5	91	28.9
3	307	87.9	197	62.5
4	0	0	1	0.3

[a] Early nests in 1979 were those in which the first egg was laid on 5 June or earlier. In 1980 the cut-off date was 3 June, the median date of egg laying (see Fig. 2).

TABLE 2. Mean weight (g) of eggs in 1979 and 1980.

		a eggs		*b* eggs		*c* eggs	
	n	x̄	SD	x̄	SD	x̄	SD
1979							
3-egg clutches	54	94.8	8.44	92.4	7.74	86.1	7.34
1980							
3-egg clutches	150	95.7	7.74	95.0	7.19	87.8	7.06
2-egg clutches	26	92.6	9.25	89.3	7.33		

results are reported for several other species of gulls (Barth 1967, Schreiber et al. 1979). In 1980, *a, b,* and *c* eggs averaged heavier than their respective counterparts in 1979 (Table 2), but only *b* eggs were significantly ($P < 0.05$) heavier than those in 1979.

In 2-egg clutches in 1980 (Table 2), the mean weights of *a* and *b* eggs were not significantly different from each other. Additionally, *a* and *b* eggs in 3-egg clutches in 1980 were not significantly heavier than their counterparts in 2-egg clutches (Table 2).

Although the mean weight of *a, b,* and *c* eggs in late clutches was consistently lighter than their respective counterparts in early clutches (Table 3), the differences were not significant ($P > 0.05$). A decline in mean weight of fresh eggs through the season has been shown in other species of gulls (Mills 1979, Parsons 1972).

The mean weight of eggs in the densely populated meadow 1 (*a* egg = 95.5 ± 7.1 g, *b* egg = 95.1 ± 7.0, and *c* egg = 88.0 ± 6.7, $n = 97$) did not differ significantly ($P > 0.05$) from that in the relatively sparsely populated meadow 3 (96.1 ± 8.7 g, 94.9 ± 7.4, and 87.4 ± 7.6, respectively, $n = 53$). The eggs of meadow 9 and 11 (Fig. 1) were not weighed.

Egg size.—The mean length and width of *a, b,* and *c* eggs in 1980 are presented in Table 4. In 3-egg clutches, *a* and *b* eggs did not differ significantly in mean length and width, but *a* and *b* eggs were significantly longer ($P < 0.001$) and wider ($P < 0.001$) than *c* eggs. The mean

TABLE 3. Mean weight of eggs in early versus late nests in 1979 and 1980.[a]

		a egg		*b* egg		*c* egg	
	n	x̄	SD	x̄	SD	x̄	SD
1979							
Early nests	35	95.2	9.06	93.5	8.20	87.0	7.53
Late nests	19	94.1	7.05	90.4	6.33	84.5	6.68
1980							
Early nests	95	96.0	7.36	95.4	6.88	88.2	6.82
Late nests	55	95.2	8.32	94.5	7.67	87.1	7.41

[a] Early and late as defined in Table 1.

TABLE 4. Mean length (mm) and width (mm) of eggs of Glaucous-winged Gulls in 1980 in 2 and 3-egg clutches.

		a eggs		*b* eggs		*c* eggs	
	n	$\bar{x}$	SD	$\bar{x}$	SD	$\bar{x}$	SD
2-egg clutches							
Length	28	71.2	2.90	70.1	2.67		
Width	28	49.4	1.79	48.7	1.57		
3-egg clutches							
Length	144	71.6	2.67	71.3	2.56	69.5	2.77
Width	144	49.8	1.53	49.7	1.49	48.2	1.46

length and width of *a* and *b* eggs in 2-egg clutches were not significantly different from each other. The *a* eggs in 2 and 3-egg clutches did not differ significantly from each other in length or width, but *b* eggs in 2-egg clutches were significantly ($P < 0.001$) narrower than *b* eggs in 3-egg clutches. Similar results were found by Schreiber et al. (1979).

Laying interval between eggs.—For 3-egg clutches ($n = 322$) the mean interval between *a* and *b* eggs was 2.19 ± 0.61 d, which was significantly shorter (χ^2 test, $P < 0.001$) than the interval between *b* and *c* eggs (2.37 ± 0.54 d). The difference amounts to 4 h and 32 min. The mean interval between *a* and *c* eggs was 4.61 ± 0.69 days or 110.6 h.

In 1979 and 1980 the mean laying interval between *a* and *b* eggs in 3-egg clutches was significantly shorter (Wilcoxon test, $P < 0.001$) than the same interval in 2-egg clutches (Table 5). Similar results were found in Laughing Gulls (*L. atricilla*) (Schreiber et al. 1979) and Dominican Gulls (*L. dominicanus*) (Fordham 1964). Apparently, females that lay 2-egg clutches not only lay significantly smaller and lighter eggs than females that lay 3-egg clutches, but also they lay *b* eggs at significantly longer intervals after the *a* egg than females that lay 3-egg clutches.

The mean intervals in days between the laying of *a* and *b* eggs and *b* and *c* eggs in early and late clutches (Table 6) were not significantly different ($P > 0.05$), as is the case in Laughing Gulls (Schreiber et al. 1979).

Incubation period.—The incubation period is defined as the number of days that have elapsed from when the egg was laid until the chick has emerged from that same egg. In 1979 and 1980, *a* eggs had significantly

TABLE 5. Mean interval (in days) between laying of *a* and *b* eggs in 2-egg clutches and 3-egg clutches in 1979 and 1980.

	2-egg clutches			3-egg clutches		
Year	*n*	$\bar{x}$	SD	*n*	$\bar{x}$	SD
1979	46	2.80	0.71	198	2.16	0.60
1980	57	2.80	0.83	322	2.19	0.61

TABLE 6. Mean interval (in days) between laying of *a* and *b* and between laying of *b* and *c* eggs in early and late nests in 1980.[a]

Interval (days)	*a–b* eggs				*b–c* eggs			
	Early		Late		Early		Late	
	n	x̄	*n*	x̄	*n*	x̄	*n*	x̄
1	20		12		3		1	
2	115		82		117		84	
3	52		41		63		48	
4	1		0		4		2	
Total	187	2.17	135	2.21	187	2.36	135	2.38

[a] Early and late as defined in Table 1.

longer incubation periods than *b* eggs ($t = 10.77$, $P < 0.001$, and $t = 11.90$, $P < 0.001$, respectively) and *c* eggs ($t = 15.09$, $P < 0.001$, and $t = 21.77$, $P < 0.001$, respectively) (Table 7). In 1979 and 1980 *b* eggs had significantly longer incubation periods than *c* eggs ($t = 4.82$, $P < 0.001$, and $t = 7.91$, $P < 0.001$, respectively) (Table 7). The mean incubation period of *a, b,* and *c* eggs for both years combined was 28.4 ± 1.58 d ($n = 354$). Full incubation does not start until the *c* egg is laid (Drent 1970, Vermeer 1963).

Although the incubation periods of *a, b,* and *c* eggs in early nests were generally longer than those of late nests (Table 7), the differences were not significant ($P > 0.05$). MacRoberts and MacRoberts (1972) and Parsons (1972) found a seasonal decrease in the length of the incubation period in Herring Gulls, which they showed to be related to changes in nest attentiveness and ambient temperature, and egg size, respectively.

Hatching success.—The number of eggs hatching in 3-egg clutches in 1979 was significantly higher ($P < 0.001$) than in 1980 (Table 8), and there was no statistical difference between the hatching success of *a, b,*

TABLE 7. Mean incubation periods of early and late nests and all nests combined of Glaucous-winged Gulls in 1979 and 1980.

	a egg			*b* egg			*c* egg		
	n	x̄	SD	*n*	x̄	SD	*n*	x̄	SD
1979									
Early[a]	25	29.9	0.77	23	28.0	0.69	22	27.0	0.80
Late	14	29.9	0.80	16	27.8	0.66	17	27.1	0.66
All	39	29.9	0.78	39	27.9	0.69	39	27.1	0.75
1980									
Early	43	30.6	0.97	49	28.7	1.09	44	27.2	0.93
Late	36	29.9	0.98	37	27.9	0.87	37	26.9	0.62
All	79	30.3	1.03	86	28.3	1.09	81	27.1	0.82

[a] Early and late as defined in Table 1.

TABLE 8. Hatching success and fate of eggs that did not hatch in 2- and 3-egg clutches of Glaucous-winged Gulls in 1979 and 1980.

	2-egg clutches				3-egg clutches			
	1979		1980		1979		1980	
	n	%	*n*	%	*n*	%	*n*	%
Total no. of eggs	28		30		162		246	
Hatched	20	71	22	73	135	83	171	70
Disappeared	1	4	2	7	7	4	16	7
Failed to hatch	7	25	4	13	16	10	49	20
Died hatching	0	0	2	7	4	3	10	4
Total no. of nests	14		15		54		82	

and *c* eggs in either year ($P > 0.05$). Lower hatching sucess on Mandarte Island in 1980 than in 1979 may have been the result of record breaking precipitation, which caused periodic flooding of some nests.

Hatching success of 2-egg clutches in both years was lower than in 3-egg clutches in 1980 but not in 1979 (Table 8). Lower hatching success in 2-egg clutches than in 3-egg clutches has been reported for other species of gulls (Fordham 1964, Schreiber et al. 1979). My sample sizes for 2-egg clutches are too small to discuss them in this context.

DISCUSSION

When the breeding population of Herring Gulls on the Isle of May, England was reduced to one quarter, the egg size increased and more young were raised than before, but the mean clutch size remained the same (Coulson et al. 1982). In contrast, de Witt and Spaans (1984) showed that when the population of Herring Gulls increased 3-fold, territory size, clutch size, egg volume, growth rates, and breeding success decreased. I found that despite a 3-fold increase in the Glaucous-winged Gull population in British Columbia (Campbell 1975) the mean internest distance on Mandarte Island in 1980 did not change significantly from what it was in 1962 (Table 9). Apparently the additional birds have started new colonies (Campbell 1975) or gone to other colonies. In addition, mean clutch size, laying interval between the *a* and *c* eggs, incubation period of the *c* eggs, and hatching success did not differ substantially from data obtained by Vermeer (1963) (Table 9).

It appears that nest density in Herring Gulls influences the size of various reproductive parameters (de Witt and Spaans 1984). However, in the Mandarte Island colony, mean clutch size and egg size on Meadow 1 (Fig. 1) did not differ significantly from that on the more sparsely inhabited meadows 3 and 9 combined. Thus nest density *per se* appears not to influence egg size or clutch size in Glaucous-winged Gulls on Mandarte, at least not at current densities (Fordham 1970, Patterson 1965, see also Vermeer 1963).

De Witt and Spaans (1984) assumed that the negative relationship

TABLE 9. Nesting parameters in this study compared with those in Vermeer (1963).

	Vermeer		This study	
	x̄ ± SD	*n*	x̄ ± SD	*n*
Internest distance (m)	2.60[a] ± ?	193	2.64 ± 1.24	247
Clutch size	2.82 ± 0.42	479	2.69 ± 0.59	297[b]
			2.77 ± 0.47	417[c]
Laying interval (*a–c* egg) (d)	4.59 ± 0.60	91	4.61 ± 0.69	321
Incubation period of *c* egg (d)	26.90 ± 0.91	128	27.00 ± 0.79	120
% Eggs hatched	71% (1961)		83% (1979)	
	83% (1962)		70% (1980)	

[a] Calculated from figure 13 in Vermeer 1970.
[b] 1979.
[c] 1980.

between nest density and reproductive success is influenced by the size of the territory, the resulting increased aggression, and the greater tendency of the young to wander off the territory. Nest density on Mandarte was far greater (Vermeer 1963, this study Table 9) than reported for Herring Gulls by de Witt and Spaans (1984). Rather than nest density *per se,* the adequacy of the food supply relative to numbers of gulls may be more important. Schreiber et al. (1979) reported that the egg size and clutch size of Laughing Gulls decreased in size with an increase in nest density. They suggest, however, that this may be due to changes in the food supply or feeding habits rather than density of nests as such. Coulson et al. (1982) suspected that competition for food and space with increased population size results in decreased body and egg size. When the food supply of Dominican Gulls (*L. dominicanus*) declined, chick mortality due to attacks by adults increased (Fordham 1970). Hungry chicks may wander more than well-fed ones and may therefore be more prone to being killed by neighboring adults (Hunt 1972, Hunt and Hunt 1976, Ward 1973).

Parsons (1975), Mills (1979), and Schreiber et al. (1979), among others, showed that chicks hatching from small eggs have significantly less chance of surviving than their siblings from large eggs. The maximum, normal clutch size in *L. glaucescens* and that of most other species in the genus *Larus* is 3 eggs, which corresponds with the prescence of 3 separate brood patches. Coulson et al. (1982) found that when the Herring Gull population was reduced to one quarter, the clutch size remained the same but the egg size increased resulting in a better productivity. However, when the food supply of Arctic Terns (*Sterna paradisaea*) was inadequate, there was a change in the clutch size rather than the egg size (Coulson and Horobin 1976). In contrast, de Witt and Spaans (1984) found that a 3-fold increase in their study population of Herring Gulls resulted in a reduction of clutch size *and* egg volume. However, it would appear from their data (de Witt and Spaans 1984), that difference in mean egg volumes (not statistically tested by them) may not be sig-

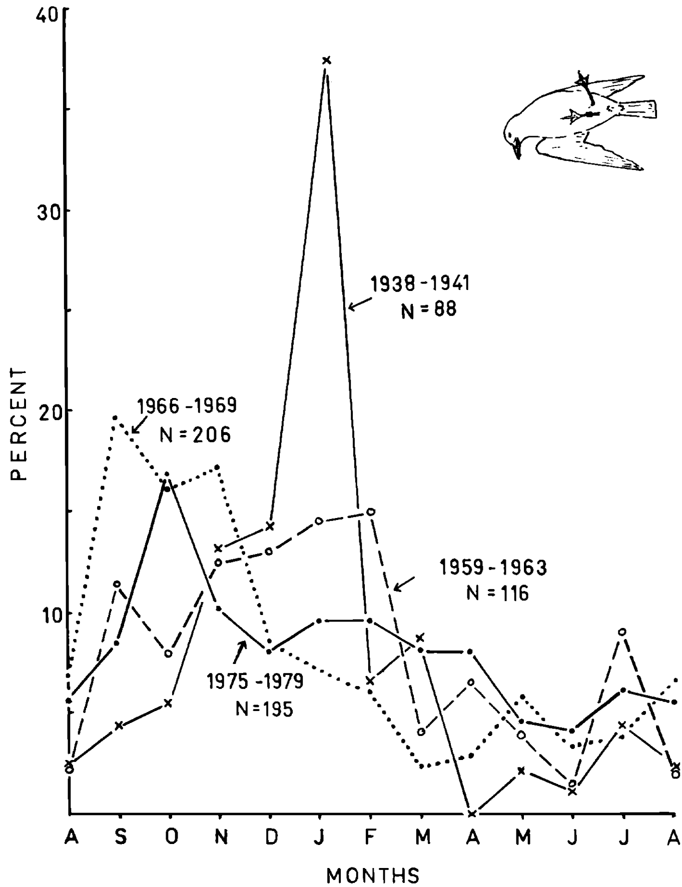

FIGURE 3. Seasonal occurrence of dead, 1-yr-old Glaucous-winged Gulls banded in British Columbia and recovered in western North America, expressed in percentage/mo of annual mortality. For each curve the sample size and the years in which the birds were banded is shown.

nificant. In my study, clutch size was significantly larger in early nests than in late ones (Table 2), but egg weight in early and late nests did not differ significantly (Table 5). Similarly, the laying interval between *a* and *c* eggs in early nests was not significantly different from that in late nests (Table 8). Furthermore, birds that had a long laying interval (5 d between the laying of the *a* and *c* eggs) or a short laying interval (4 d) showed no significant ($P > 0.05$) difference in mean egg volume. This strongly suggests that individuals that find it difficult to obtain enough energy for egg production simply spent more time to acquire that energy.

The absence of significant changes in the various nesting parameters in this study as compared to Vermeer's (1963) suggests that the food supply, despite the increase in the Glaucous-winged Gull population in British Columbia, is still adequate, at least in the early part of the breeding season. There are indirect indications, however, that the food supply at other times, including perhaps the latter part of the breeding season, may no longer be adequate.

Glaucous-winged Gulls in British Columbia have been banded on and off since 1938. Woodbury and Knight (1951) showed that peak mortality of less-than-1-yr-old birds, banded in 1938–1941 and recovered away from the colonies, occurred in January (Fig. 3). This pattern was still present in birds that were banded in the early 1960s (van Tets 1968) although the peak was less pronounced and more broadly based, beginning in November (Fig. 3). Recoveries of birds less than 1-yr-old, banded in the period 1966–1969, and 1975–1979, show that the peak of mortality has continued to move from mid-winter to the late summer and early-fall (Fig. 3). This suggests that the food supply in the early autumn is no longer adequate to meet the demands of the adults and the recently fledged young, the latter losing out in the resulting competition. Competition with adults may also have an effect on the survival of less than 1-yr-old birds during May to August of the year following fledging. Percent mortality of this age class was consistently higher in these months than in Woodbury and Knight's (1951) and van Tets' (1968) study, except in July.

SUMMARY

The population of Glaucous-winged Gulls in British Columbia has doubled between 1960 and 1974. It was assumed that this increase would have resulted in a decrease in egg size, clutch size, incubation period, and hatching success, and an increase in the laying interval between eggs in a clutch. A comparison of data obtained on Mandarte Island in 1961–1962 and 1979–1980 does not support the assumption. The additional birds apparently exploit food sources that have heretofore been largely untapped. Indirect indications are, however, that the food supply at other times, particularly the later part of the breeding season, may no longer be adequate, because the peak of mortality of birds less than 1-yr-old has shifted from mid-winter prior to the population increase to early autumn at present.

ACKNOWLEDGMENTS

I am indebted to L. Graf, L. Legendre, and A. Stuart for assistance in the field and to J. N. M. Smith for his help and cooperation. I very much appreciate the help I received from R. W. Campbell who provided me with the banding records. Permission to do the research on Mandarte Island was granted by the Tsawout and Tseycum Indian Bands of Saanich, British Columbia. The study was supported by the National Sciences and Engineering Research Council of Canada.

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