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HYBRIDIZATION BETWEEN GULLS (LARUS GLAUCESCENS AND L. OCCIDENTALIS) IN THE PACIFIC NORTHWEST

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ABSTRACT.—Interbreeding between Glaucous-winged Gulls (*Larus glaucescens*) and Western Gulls (*L. occidentalis*) occurs extensively within a 180-km zone along the Washington coast, producing a high frequency of intermediate morphs in breeding populations. We conducted intensive studies on Destruction Island, Washington, in the midst of the zone of hybridization. There over half of the breeding birds were phenotypically intergrades between pure Glaucous-winged and Western gulls in characters of iris and eye-ring coloration, mantle shade, and wing tip pattern. Mating patterns of Destruction Island gulls were assortative, individuals pairing with mates similar to themselves. Pairs composed of pure Glaucous-winged or Western gulls hatched significantly fewer eggs than pairs containing at least one hybrid individual. The greater apparent reproductive success of the intergrades would seem to be countered by the assortative mating patterns, possibly providing conditions sufficient to maintain an equilibrium system containing both pure types as well as intergrades. These conditions are explored in a simulation model that considered immigration, density-dependent fecundity, pairing and reproduction, and mortality. A stable colony of mixed composition may be maintained by a regular but small influx of pure types into the colony. *Received 11 April 1977, accepted 15 June 1977.*

STUDIES of hybridization zones in nature are of major interest in assessing the evolutionary status of closely related populations (Moore 1977). The biological species concept (Mayr 1940, 1942) proposes that the best criterion for defining species of sexual organisms is the reproductive behavior of the organisms themselves. If members of two populations interbreed freely and successfully wherever they come into contact, the taxonomist should respect their "judgement" and classify them as conspecifics. Conversely, if members of the two populations forego the chances to interbreed and consistently mate assortatively, they should be considered separate species. Studies of situations where some hybridization is regular (e.g. Sibley and Short 1959, Short 1965) have been largely extensive in nature. More intensive investigations within hybridization zones are necessary for an understanding of the evolutionary history and potential of specific situations, and may also increase our understanding of speciation.

Hybridization occurs in varying frequencies between many of the large gulls of the *Larus argentatus* species group (Tinbergen 1953, Williamson and Peyton 1963, Harris 1970, Ingolfsson 1970, Jehl 1971, Patten and Weisbrod 1974). Forms in this

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group are morphologically similar, differing mainly in size, mantle and wing tip color, eye color, and allometric details of bill structure. On the west coast of North America, from the Aleutian and Pribilof islands and the southern Bering Sea coast south to the central Washington coast, the Glaucous-winged Gull (*Larus glaucescens*) is the breeding representative of the group. To the south, from the southern Washington coast to Baja California, it is replaced by the Western Gull (*L. occidentalis*). In south-central Alaska the Glaucous-winged Gull interbreeds with Herring Gulls (*L. argentatus smithsonianus*). Here Glaucous-winged colonies are coastal, while those of Herring Gulls are primarily inland on freshwater lakes and rivers, and hybridization appears to occur mostly at the heads of bays and fjords where the two forms meet (Williamson and Peyton 1963, Patten and Weisbrod 1974).

Dawson (1909) first explored the seabird colonies of the outer Washington coast and found evidence of extensive hybridization of Glaucous-winged and Western gulls around Carroll Island. Pearse (1946) noted possible hybridization on the outer coast of Vancouver Island. The range of overlap and hybridization between these gulls was reviewed by Scott (1971), who found mixed pairs of Western and Glaucous-winged gulls as far south as Yaquina Head, Oregon, and extensive hybridization at Destruction Island, Washington. We surveyed the gull colonies of the outer Washington and northern Oregon coasts to determine more precisely the extent and range of overlap and hybridization. We also studied the morphology, mating patterns, and reproductive success of the birds in the colony on Destruction Island, Washington, in the area of most extensive hybridization. Finally, we have used data on mating patterns and hatching success collected at Destruction Island as inputs to a computer simulation designed to evaluate the possible evolutionary consequences of the hybridization.

THE EXTENT OF HYBRIDIZATION

We made counts of adult Glaucous-winged, Western, and intermediate gulls using binoculars and spotting scope in the accessible colonies of the outer Washington and northern Oregon coasts in 1974 and 1975 (Table 1, Fig. 1). The phenotypes of all birds occupying territories were recorded to the extent possible under the distance constraints. Mantle and wing tip color could be recorded for birds at 30 colonies and eye colors could also be recorded for birds at many of these. The ends of the survey area are defined by gaps in the gulls' breeding range. Cape Flattery is at the entrance to the Straits of Juan de Fuca, so there is a gap of at least 40 km to the nearest colony on Vancouver Island, British Columbia, and the colonies near Florence, Oregon are separated by 87 km of unsuitable habitat from the nearest colonies to the south.

Extensive hybridization occurs in the region from Alexander Island to the Columbia River, a distance of 180 km. To the north of this zone the colonies consist predominantly of Glaucous-winged Gulls, while Western Gulls predominate to the south (Fig. 1). The zone appears to have shifted south in recent years. Western and intergrade gulls apparently formed a much larger part of the colonies north of La Push in the past; apparently Western Gulls were also much more prevalent on Destruction Island in 1909 (Dawson 1909, Pearse 1946). Glaucous-winged Gulls and intergrades were first noticed breeding in Oregon in 1969 (Scott 1971) but our survey indicates that they are present in small numbers in most of the northern colonies. It seems unlikely that the extensive investigations of Gabrielson and Jewett (1940)

TABLE 1. Gull colony survey. The colony numbers correspond to the numbers on Fig. 1. The starred (*) colonies were surveyed in 1974; all others were surveyed in 1975

Colony	Num-ber	Sample size	West-ern	Hybrid	Glau-cous-winged	Pre-cision[a]
Cape Flattery	1	300	22	5	275	2–3
Bodelteh I.	2	250	—	—	250	3
Bald I.	3	120	1	5	115	3
Cake I.	4	80	—	3	77	3
Unnamed rock	5	60	—	4	55	3
James I.	6	24	2[b]	—	22	2
Quilleute Needles	7	65	1	3	61	2
Toleak Pt. Rock*	8	20	—	—	20	3
Round I.*	9	150	—	10–15	140	3
South Round I.*	10	35	—	5	30	3
Half Round I.*	11	40	—	15	25	3
Alexander I.*	12	350	20	50	280	2
Ruby Beach Rock	13	2	—	2	—	1
South Rock, Hoh R.	14	8	2	5	1	2
Destruction I.*	15	162[c]	47	84	31	1
Pt. Grenville Rock	16	17	6	5	6	1
Goose I.[d]	17	106	46	43	17	1
Sand I.[d]	18	30	7	19	4	1
Whitcom I.[d]	19	30	12	17	1	2
Sand I.[e]	20	16	7	5	4	1
Ecola St. Pk.	21	30	29	—	1	2
Haystack Rock	22	150	145	4	1	1–2
Rock S. of Cannon Beach	23	73	73	—	—	1
Cove Beach Rock	24	46	39	2	5	2
Cape Meares	25	34	32	—	2	1–2
Cape Foulweather	26	25	25	—	—	1–2
Yaquina Head	27	49	47	1	1	1
Seal Rocks	28	4	4	—	—	1–2
Parrot Rock	29	36	34	1	1	1–2
Sea Lion Caves	30	79	76	3	—	1

[a] A measure of the quality of the separation, related to the distance of observation. 1 = all characters used, 2 = eye color as a whole used but ring and iris colors not separated, 3 = only mantle and tip colors used
[b] The two Western Gulls are paired to each other
[c] These are the study plot mating pattern data
[d] These colonies are on sandy islands in Gray's *Harbor*, Wash.
[e] This Sand I. is in Gray's *Bay*, a part of the Columbia River estuary near Chinook, Wash.

and of William L. Finley would have failed to report Glaucous-winged Gulls if they had been breeding. On the other hand, Dawson's (1909) observations indicated that hybridization was occurring commonly on the Olympic Peninsula as long ago as 1900.

METHODS

Following Scott's (1971) survey, the large mixed colony on Destruction Island was chosen for intensive study. The gull colony occupied sandstone platforms around the margin of the western half of the island, grassy slopes at the northwest and southwest points, and a log-covered gravel beach. The largest and densest sections of the colony occupied two low rocky fingers that extended west from the northwest and southwest points of the island. We established four study plots to sample the range of habitats used for breeding; together these plots contained 96 active nests, or about 20% of the total colony. Brief visits also were made to a Western Gull colony on Southeast Farallon Island, California, and to a Glaucous-winged Gull colony on Greater Chain Island near Victoria, British Columbia, to gather comparative information.

Originally we attempted to capture by cannon-netting, measure, and individually mark a large pro-portion of the adult gulls at Destruction Island to determine the mate preference patterns and the extent of intergradation in the population. However, in 1974 we decided that difficulties with cannon-netting (resulting largely from the gulls' remarkable memory of the net), our inability to sample the mixed
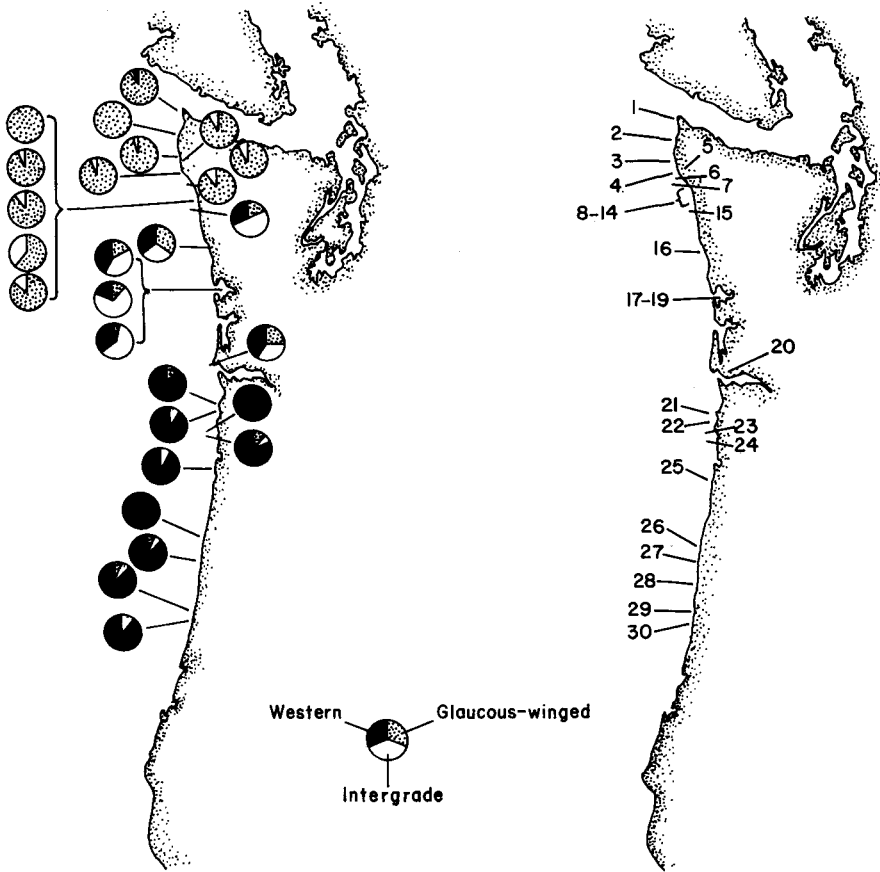
Fig. 1. Frequencies of Western, Glaucous-winged, and intergrade gulls at breeding colonies on the Oregon and Washington coast, as revealed in 1974–75 surveys. Colony locations numbered on the right are listed in Table 1. Colonies containing fewer than 10 individuals are not shown. Destruction Island is number 15; the village of La Push is adjacent to number 6.

population randomly, and band-loss problems made this approach unsuitable. Therefore, in 1974 we assessed visually the variable color characters of all adults in attendance at the 96 nests in the four plots by studying the birds carefully through a 20–45× spotting scope. This phenotype assessment was done over a period of 15 days beginning just after the earliest eggs hatched. Periods of recording were limited to a maximum of 90 min, separated by at least 120 min to avoid error from eye fatigue. Observations were made only under favorable light conditions (high thin overcast or sunny), never against the light, and only between 0800 and 1700.

Iris coloration was recorded on a scale of 1 to 5, with 1 = the iris so dark that it does not contrast with the pupil, and 5 = yellow with only slight flecking. For the eye-rings, the presence or absence and the intensity of yellow and of purple pigment were recorded. Intensity was estimated in three classes. Wing tip and mantle shades were estimated on the same gray scale used for captured birds. The pattern of white spotting in the wing tips was not used because it clearly does not vary clinally (contra Ingolfsson 1970) and because it could not be recorded easily for sitting birds. These color recordings were basically the same as those taken on the cannon-netted birds, which were compared directly to a Villalobos color chart (Palmer 1962) for eye characters and to a Kodak density-calibrated neutral gray scale for wing tip and mantle colors. Those individually-banded and hand-measured birds present on the plots were used frequently as color references for uncaptured birds. This was most important for assessing mantle shade, which changed markedly with the angle of the bird to the sun.

We analyzed the patterns of plumage and eye color variation in the Destruction Island gulls by two

parallel methods, Hybrid Index (Sibley 1961; Mayr 1963, 1969; Short 1969) and Manhattan Distance (Sneath and Sokal 1973). The latter method was equal or superior to Hybrid Index in sensitivity, power, and clarity in all of our applications. The Hybrid Index results will be used here only for the comparison of the Destruction Island gulls to the samples from Greater Chain and Southeast Farallon islands. A detailed comparison of these methods will be published separately (Hoffman unpublished).

Manhattan Distance is a multivariate measure of the morphological "distance" between members of a population. It was used instead of the more popular Taxonomic (Euclidian) Distance because it distinguishes individuals differing greatly in one character in comparison to a standard reference from individuals differing moderately in several characters. This difference makes Manhattan Distance more sensitive to presumed genetic differences between individuals. Individuals that differ moderately in several characters should possess different alleles at more loci than individuals that differ greatly but in only one character (assuming separate genetic control for the different characters—see the analysis of independence of variation below). This analysis used the 53 pairs of birds from the four study plots for which both members were completely described. The data were statistically standardized (transformed so that the distribution of each has a mean of zero and a standard deviation of 1.0), and a 106 × 106 similarity matrix was calculated, using the *MINT numerical taxonomy program series of Rohlf (1971). The matrix contains comparisons ("distance" measures) of each bird with all other birds in the sample. Values ranged from zero (identical) to 2.5 (the two birds differing the most).

The Manhattan Distance analysis was used to test the hypothesis that mating in the Destruction Island colony is not random with respect to the variable plumage and eye color characters. In this analysis, the similarity matrix consists of all possible pairwise combinations of birds. The main diagonal consists of birds compared to themselves, and was discarded. The distances between members of the pairs appear as the alternate members of the first subdiagonal. These were collected, the mean and variance were calculated, and the distances were plotted (Fig. 2).

This mean was statistically compared to the mean of the whole subdiagonal region of the similarity matrix. The unpaired t-test (two-tailed) used assumes that samples were taken from a population with a normal distribution. The actual distribution is similar to normal but with the lower tail mildly truncated. We assumed that the characters used are uniformly distributed between the sexes. Sex-linked deviations from uniformity in the distribution of the characters would cause the expected within-pairs Manhattan Distances to be larger than calculated. Thus, any tendency toward assortative mating would be slightly underestimated by these analyses, and any tendency toward disassortative mating would be overestimated.

Each nest in the four Destruction Island study plots was monitored on alternate days to determine the timing and success of hatching. Time constraints and the inability to determine unequivocally the parentage of young gulls after they left the nests prevented measurement of fledging success. Clutch size, hatching success, and egg inviability were tabulated for each of the six pair categories (Wn × Wn, Wn × Hyb, Wn × GW, Hyb × Hyb, Hyb × GW, GW × GW). An analysis of variance (ANOVA, Snedecor and Cochran 1969) was used to test the significance of the observed differences between classes in numbers of eggs hatching per nest.

RESULTS

MORPHOLOGICAL ANALYSIS

Because Glaucous-winged and Western gulls overlap extensively in body measurements (Dwight 1925) we used colorimetric characters alone for separation of the various types. All of our analyses of these color characters are restricted to consideration of breeding adult birds. Typical *Larus occidentalis occidentalis* have white heads and bodies, yellow to orange eye-rings, a yellow iris with a light covering of brown flecks of melanin, a fairly dark bluish-gray mantle (0.7 to 0.8 on the gray scale used) and black wing tips with white apical spots and one or two white "mirrors." A typical Glaucous-winged Gull has a white head and body, magenta or purple eye-rings, dark brown irises, a light gray or bluish-gray mantle (gray scale value of 0.3 to 0.4) and pale gray wing tips with two or three white "mirrors" and apical white spots. The secondaries and inner primaries of all of these gulls are broadly tipped with white.
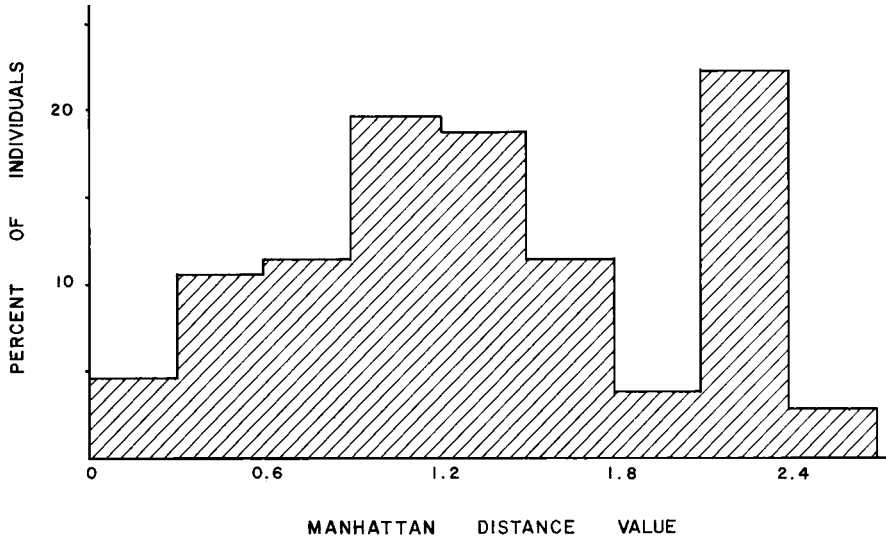
MANHATTAN   DISTANCE   VALUE

Fig. 2. Frequency distribution of Manhattan Distance scores of Destruction Island gulls. The distance values are plotted in relation to the Glaucous-winged Gull with the purest set of characters (value of 0).

In the intergrades, intermediate variation can be found in all of the color characters distinguishing the two typical forms. Iris color varies from yellow with light melanin flecking through intermediate stages with a heavier covering of flecking to the *L. glaucescens* type with the yellow base color completely obscured by the overlying melanin granules. These brown flecks vary both in size and in density, but iris color was recorded as percent cover, as if the variation were clinal in a single character. Two separate pigment systems are present in the eye-rings, a yellow or orange, and a purple. Intergrades may have purple or magenta eye-rings as in *L. glaucescens*, yellow or orange as in *L. occidentalis*, white, white with either pink or yellow highlights, or yellow with pink highlights.

Wing tip color varies continuously from pale gray to black. The extent of the dark pigment (when it is present) is also variable, with the gray of intermediate individuals' wing tips frequently restricted to a small area at the tips. The wing tip pattern of white "mirrors" and apical spots has a wider range of variation in the intergrades than in either parental type. Some intergrades have no white "mirrors" and greater reduction of the apical spots than either parental form, and some have more white in the "mirrors" and more and larger spots than either. In all birds examined, the gray or black of the wing tips graded into the mantle gray without an intervening white area as in *L. thayeri* and *L. schistisagus*.

Table 2 contains correlation coefficients for the within-individual correlations of

TABLE 2. Correlation coefficients between the characters used in the morphological analysis

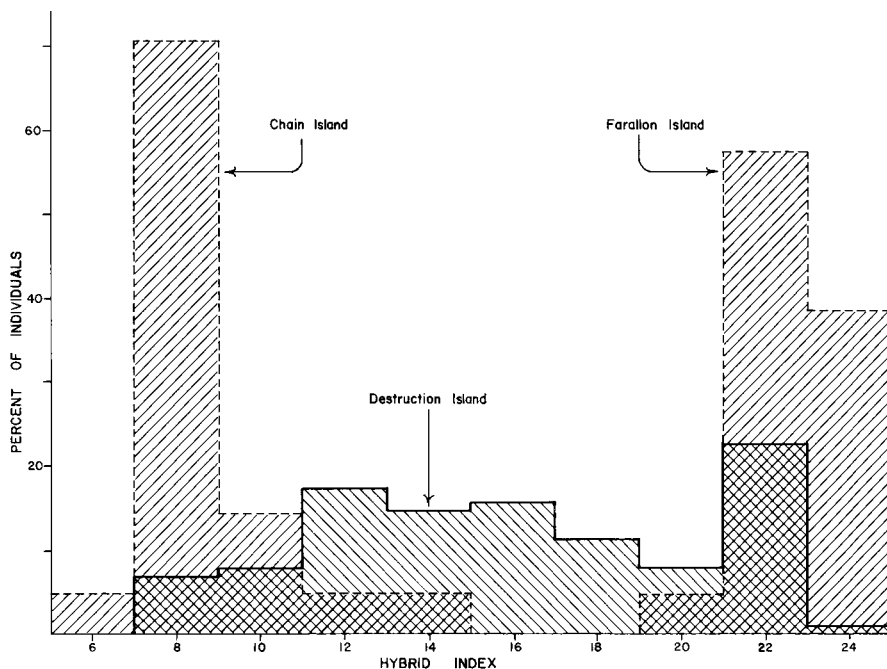|	Iris	Eye-ring pigments		Mantle
		Yellow	Purple	
Iris				
Yellow	0.20			
Purple	0.23	−0.89		
Mantle	0.58	0.36	0.30	
Tips	0.59	0.36	0.32	0.82

Fig. 3. Frequency distribution of Hybrid Index values for gull samples from Greater Chain Island, British Columbia, Southeast Farallon Island, California, and Destruction Island, Washington.

the variations in the traits just outlined. Mantle and wing tip shades are highly correlated, but most of the other characters show weaker correlations. As the population sampled was not normal, but instead contained about one-half intergrades and about one-half pure parental types (with all characters highly correlated by genetic fixation), traits that are genetically unlinked should show correlations of about 0.4 to 0.5. The strong negative correlation between yellow and purple eye-ring colors indicates that usually one or the other pigment is present, but the degree of negative correlation is inflated by scoring errors among those birds with both pigments. The birds with both pigments were more frequent in the sample of captured birds (which was biased) than in the plot samples used in this analysis. Such errors have a small conservative effect on the statistical analyses below, so the frequency and extent of intergradation are slightly underestimated.

The Manhattan Distance analysis provides quantification of the intergradation just described qualitatively. The histogram of Manhattan Distances (from the most extreme or pure Glaucous-winged Gull) exhibits a bimodal distribution (Fig. 2). One mode consists of intergrades and the other of Western Gulls. The two modes are separated by a gap, which indicates a scarcity of "almost" Western Gulls. The Hybrid Index analysis yields a qualitatively similar but clearer graphical representation of the relationships of the Destruction Island sample to the Greater Chain Island and Southeast Farallon Island samples (Fig. 3). The Chain Island distribution shows a tail representing birds with some degree of darkening of the primary tips. The Farallon Islands sample is less variable for these characters, although iris and mantle color do vary slightly.

TABLE 3. Manhattan Distance analysis of mating patterns. Student's t is used to compare the mean of the matrix values to the observed sample mean from the 53 pairs. **** = 99.9% level of significance

Source	N	Mean of within-pairs distances	S^2	t	d.f.
Pairs sampled	53	0.834	0.325		
Total matrix	5,565	1.097	0.309	3.43****	5,616

NEST SITE SELECTION

Glaucous-winged and Western gulls differ in their nesting substrate preferences. Most of the Western Gulls nesting on the Oregon coast occupy bare rock or occasionally short grass substrates, and the nests usually are quite exposed. Glaucous-winged Gulls in Puget Sound, British Columbia, and Alaska most frequently nest upon sand or soil substrates, in areas of taller grass. Nests often are hidden in the grass. Large colonies normally have their greatest densities on the appropriate substrate for the gulls present, but may extend onto adjacent areas of the less favored substrate. These substrate preferences may play an important role in determining the composition of colonies in the zone of contact. The colony sites north of Destruction Island are mostly grass-covered, and have primarily Glaucous-winged Gulls. The Cape Flattery colonies, with extensive areas of bare rock, have higher frequencies of Western Gulls and/or dark intermediates than several colonies to the south. Most available sites on the Oregon coast are on bare rocky islands and the colonies are composed primarily of Western Gulls. Those partially on grass, such as Sea Lion Caves and Parrot Rock, have higher frequencies of Glaucous-winged and intergrade gulls than adjacent colonies on bare rock. The colony at Pt. Grenville on the central Washington coast is on bare rock, and contains mostly Western Gulls, although the Destruction Island colony to the north of it (with both substrates) and the Gray's Harbor and Sand Island (Columbia River) colonies to the south, on vegetated sand islands, have large numbers of both Glaucous-winged and Western gulls and of intergrades. At Destruction Island, two-thirds of the pure Glaucous-winged Gull pairs were nesting in or at the edge of the grass. No more than one-third of any other class built nests in or associated with grass. These substrate preferences may be important in determining the location of the overlap zone, but are clearly not sufficient to provide isolation.

MATING PATTERNS

Table 3 contains the results of the Manhattan Distance analysis of mating patterns. Mating was highly significantly assortative ($P < .001$) (actually the deviations from normality in the statistical population used in this analysis make the probability that mating is random even lower). Thus to a significant degree the gulls choose mates similar to themselves. This tendency is general and exceptions occur regularly, but the mating patterns observed clearly indicate that the birds' mate preferences are based on general similarity in several characters and not on a single key character.

HATCHING SUCCESS

Phenotypes of both parents were determined for 81 nests in the four study plots. The three categories containing pairs with at least one hybrid parent were combined

TABLE 4. Hatching success of Destruction Island gulls, combined for the four study plots. In the Analysis of Variance, the "Pure vs. Mixed" category compares the Wn × Wn and GW × GW pairs, as a group, with the three categories containing Hybrids, as a group

Pair types	Pair types[a]						
	Wn × Wn	Wn × Hyb	Hyb × Hyb	Hyb × GW	GW × GW	Wn × GW	Σ
Pairs	11	23	25	11	9	2	81
Total eggs	27	63	69	30	20	4	213
Eggs/nest	2.45	2.74	2.76	2.72	2.22	2.00	—
Inviable eggs	7	9	13	4	4	0	37
Frequency of inviable eggs	0.26	0.14	0.19	0.13	0.20	0	0.16
Eggs hatching	20	54	56	26	16	4	176
Eggs hatching/nest	1.82	2.35	2.24	2.36	1.78	2.00	—

ANALYSIS OF VARIANCE

Source	Degrees of Freedom	Sum of Squares	Mean Squares	F ratio
Between	4	4.0042	1.0011	1.1663
Pure vs. Mixed	1	3.8015	3.8015	4.4396
Other combinations	3	0.1937	0.0646	0.0752
Within	74	63.5148	0.8583	
Total	78	67.5190		

[a] Wn = Western Gull, GW = Glaucous-winged Gull, Hyb = intergrade gulls

for analysis, as were the two categories of pure pairs. Only two nests fell into the category Wn × GW, and these were not used in the analysis. The pure pairs of Western and of Glaucous-winged gulls hatched significantly fewer eggs than pairs containing at least one hybrid individual (Table 4). This differential hatching success is caused in part by differences in the frequency of egg inviability and in part by differences in clutch size. In years of food shortage, chick mortality may be higher in large clutches, so that pure pairs might raise more of the chicks they hatch, but such compensatory mortality would be unlikely to outweigh the measured hatching success differences.

The earliest eggs in the study plots on Destruction Island hatched about 27 June and hatching continued until around 12 July. No major differences in timing were noted between the six classes of nests (Wn × Wn, etc.).

The ranges of hatching dates were very similar among the classes. The median hatching date for the Wn × Wn nests was several days earlier than the medians of the other classes, but these nests were concentrated in high-density parts of the colony, where hatching of all nests tended to be earlier.

SIMULATION OF THE ZONE OF OVERLAP AND HYBRIDIZATION

Our findings that approximately one-half of the gulls breeding at Destruction Island are of hybrid origin, that the gulls mate assortatively, and that pairs containing at least one intergrade hatched a significantly higher number of young than pure pairs, suggest the possibility that a dynamic equilibrium may exist, maintaining the system in its present intermediate state. Such an equilibrium would depend upon the tendency for the greater reproductive success of hybrids to be countered by the assortative mating patterns. Therefore, we conducted a series of computer simulations to evaluate the possible evolutionary consequences of the mate selection and nesting success patterns documented for the Destruction Island colony.
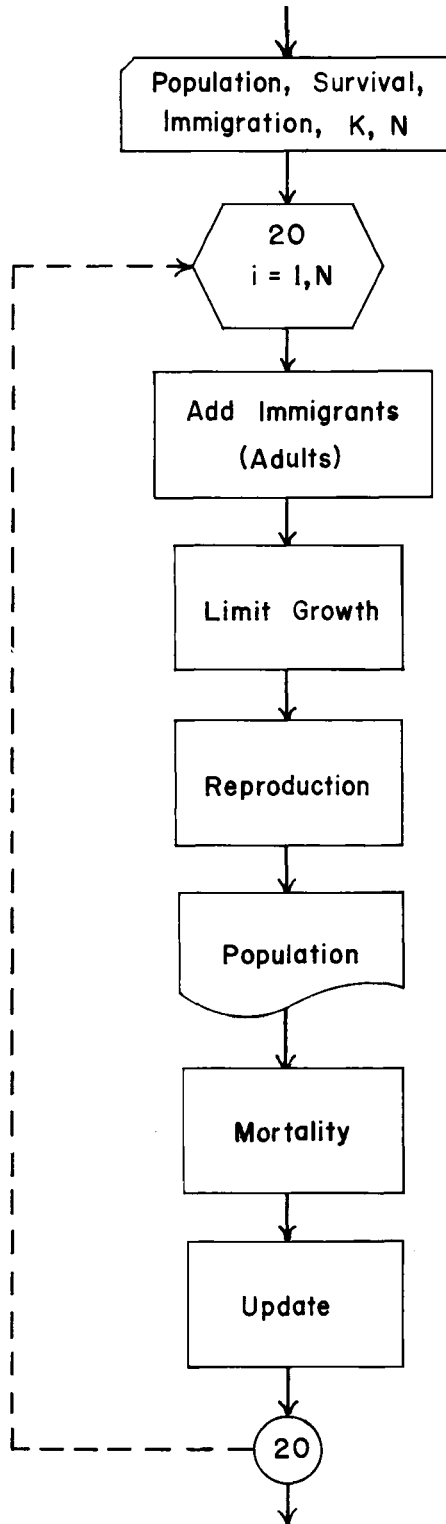
Fig. 4. Flow diagram for the computer simulation model of gull colony composition. See text.

The basic simulation is a population model of the colony, following numbers of individuals of three morphological classes (Western, Glaucous-winged, and intergrade) through time (Fig. 4). One cycle through the model represents 1 yr. Four separate subprograms are visited in turn, and handle immigration, density-dependent fecundity regulation, reproduction, and mortality in that order. Five age classes are maintained in each morphological class, because these gulls require 4 yr to mature. The immigration subprogram adds fixed numbers of Glaucous-winged and Western gulls from elsewhere to the breeding population each year. The population regulation subprogram then limits growth by density-dependent reduction of fecundity, modeled as if it resulted from crowding and associated phenomena in the nesting colony (see Tinbergen 1953). Crowding was expected to have little effect until total colony size was close to carrying capacity; therefore, we used the difference equation,

$$N_1 = cN_a[1 - (N_a/K)^\theta]$$

adapted from the single species form of the (differential) global model of growth and competition of Gilpin and Ayala (1973). N_1 is the number of young produced, N_a the total colony size (adults), c the maximum fecundity, K the carrying capacity, and θ is an interaction term that modifies the inflection point of the sigmoid curve. The value 3 was selected for the exponent θ, so the resultant growth curve is an asymmetric sigmoid with the inflection point occurring near K. As the equation is expressed, the inflection point occurs at 63% of K, but in the simulation, the 4-yr time lag elevates it to around 75–80% of K. K was set at 1,500 (the actual stable colony size reached in the model is around 1,300, depending on immigration rates).

In the reproduction subprogram, the frequencies of each of the three morphological classes in the breeding population were calculated, and the birds were paired according to the mating patterns observed at Destruction Island. Reproductive output (size of age class one) for each morphological class was calculated by multiplying the number of pairs in each of the six pair classes (Wn × Wn, Wn × Hyb, Wn × GW, Hyb × Hyb, Hyb × GW, GW × GW) by the observed hatching success at Destruction Island for that class and then subtracting one young per nest to account for nestling mortality. This brings the productivity into agreement with literature values (Kadlec and Drury 1968).

The mortality subprogram advances the age classes 1 yr and then subjects all age classes to mortality. The mortality was applied uniformly with respect to morphological classes by multiplying each age class by an age-specific survival probability. The survival probabilities (Table 5) were derived under the assumption of a stable age distribution from the Herring Gull population age structure described by Kadlec and Drury (1968).

The model contains several simplifying assumptions. It is deterministic, but with the population sizes involved, a moderate amount of stochastic variation in any of the processes will not affect the qualitative results. The model assumes no immigration of intergrades. This will be the case initially, and the assumption will be valid unless the area of hybridization expands by the outward dispersal of intergrades. The distribution of the various types (Table 1, Fig. 1) shows that the area of hybridization has not expanded greatly by the spread of intergrades. We also assumed that the measured differences in hatching success hold at least proportionally over all densities; no density-dependent principle of allocation is operating. This assumption is conservatively restrictive, since relaxation, besides making the model unwieldy, provides more opportunities for stability. K is assumed to be constant,
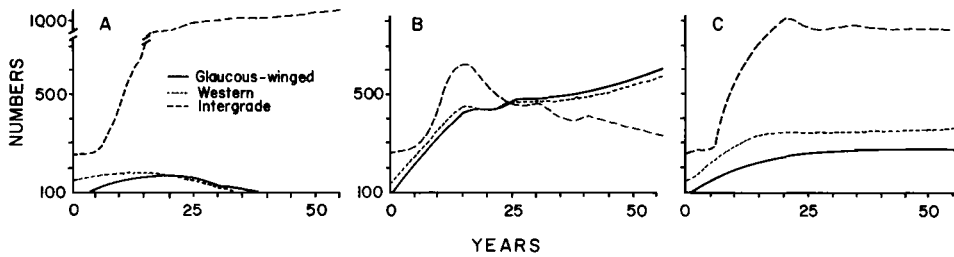
Fig. 5. Results of simulation analyses of the occurrence of gull types in a breeding colony. All simulations start with the approximate stable age distribution (Table 5). Only the adult population is shown. **A.** No immigration. **B.** Immigration rate of 30 Western and 30 Glaucous-winged gulls per year. **C.** Immigration rate of 20 Western and 13 Glaucous-winged gulls per year. The latter simulation produced the nearest approximation to the observed frequencies at Destruction Island that is possible with integer inputs of immigration rates.

but allowing K to vary would not affect the qualitative potential for intermediate equilibria. Post-hatching survival is assumed to be equal for intergrades, Western, and Glaucous-winged gulls. If intense counter-selection occurred after hatching, the potential for stable equilibria could be changed. We assumed that all of the gulls begin breeding at the same age. We were not able to collect data on the age of first breeding in this study, but have no reason to expect major differences between the forms. We assumed that population limitation is related to colony size and density, not to food supply. This is probably the normal situation for temperate and arctic seabirds (Hoffman and Wiens in prep.).

We used a variety of initial population sizes and age structures as inputs to the model to explore its behavior. We then analyzed an initial population consisting of 500 adults, together with enough younger individuals to form a stable age distribution, divided among the morphological classes in the ratio of the adult population of Destruction Island in 1974 (Table 5). Used with various immigration rates, this allowed us to discern the effects of differing immigration patterns on the stability of the system.

The results of the initial runs demonstrate that, within model constraints, a small influx of pure types into the colony can maintain the zone of overlap and hybridization. The model will produce, or maintain, a stable mixed colony as long as immigration of both Western and Glaucous-winged gulls occurs. The frequencies of both parental types in the colony are functions of the immigration rates.

Figure 5 illustrates some results of the simulation runs using the initial stable age distribution and the observed adult frequencies. If 20 Western and 13 Glaucous-winged gulls immigrate (Fig. 5C) per year, a stable equilibrium is achieved with the

TABLE 5. Inputs to the simulation analyses. The survival probabilities are calculated *from* the listed age class. The stable age distribution was derived from Kadlec and Drury (1968)

Age class (yr)	Survival probabilities	Stable age distribution		
		Wn	Hyb	GW
0	0.56			
1	0.62	32	57	21
2	0.80	20	36	13
3	0.92	16	29	11
4+	0.92	145	260	95

three morphological classes maintained in frequencies very close to those at Destruction Island in 1974. Thus, in the model population containing 1,300 adults at equilibrium these minimal numbers of immigrants can maintain Western and Glaucous-winged gulls at 29% and 19% of the adult population, respectively.

The other runs (Fig. 5, A–B) show model behavior under other immigration regimes. With no immigration the population quickly becomes dominated by hybrids, and the pure types eventually disappear. With higher immigration rates (30 Wn and 30 GW) the pure types predominate, and hybrids decline both in frequency and in number. A variety of intermediate outcomes are possible with immigration rates in the range of 10–25 individuals per species per year.

DISCUSSION

The biological species concept proposes that animal populations are organized into natural groupings of interbreeding or potentially interbreeding populations, which are presumed to share coadapted gene complexes (groups of genes at numerous loci that act in concert). Closely related and morphologically similar species are expected to differ in gene complexes to the extent that interbreeding is unfavorable, while even morphologically distinctive populations of one species possess much greater genetic similarity. Coadapted complexes are assumed to develop as population-wide responses to changing selective regimes, so the development of inter-populationally disharmonious complexes is expected to occur in geographic isolation. When divergent isolates are brought into contact, they may hybridize to some extent, depending on the degree to which morphological and behavioral divergence has provided prezygotic isolating mechanisms. Under this theoretical framework, the overlap and hybridization phase of post-contact population history will be transient, and the interbreeding of divergent populations is evolutionarily unstable. If discordant coadapted complexes have evolved in isolated populations, hybrid offspring will have reduced fitness and selection of behavioral or other prezygotic isolating mechanisms should occur rapidly. Zones of overlap with very occasional hybridization may persist, as selection may be ineffective when the frequency of hybridization is low. On the other hand, if hybrid offspring do not suffer reduced fitness the hybridization should lead to fairly rapid local swamping of population differences and mixing of the gene pools. However, if differing selective regimes persist in the populations, extensive hybridization usually should lead to the formation of a morphological cline in the divergent characters, at times in a narrow band, with the main bodies of the populations maintaining distinctiveness. The hybrid zones of *Colaptes* (Short 1965) and the *Corvus corone* complex (Mayr 1963:370, Short 1969) are good examples.

Despite their morphological differences, Glaucous-winged and Western gulls apparently have not developed gene complexes that are disharmonious or incompatible in combination. Indeed, gulls in general seem remarkably free of postzygotic barriers to hybridization. Where two or more species of the Herring Gull group co-occur, any hybrids usually seem to be viable and fertile. Herring and Glaucous gulls are sympatric with little hybridization over much of the Arctic, but are hybridizing and forming a hybrid swarm in Iceland (Ingolfsson 1970). The range of variability in Herring × Glaucous-winged hybrids in southern Alaska indicates that backcrossing must be occurring (Williamson and Peyton 1963, Patten and Weisbrod 1974, Hoffman pers. observ.). Harris (1970) has indicated that offspring of mixed pairs of
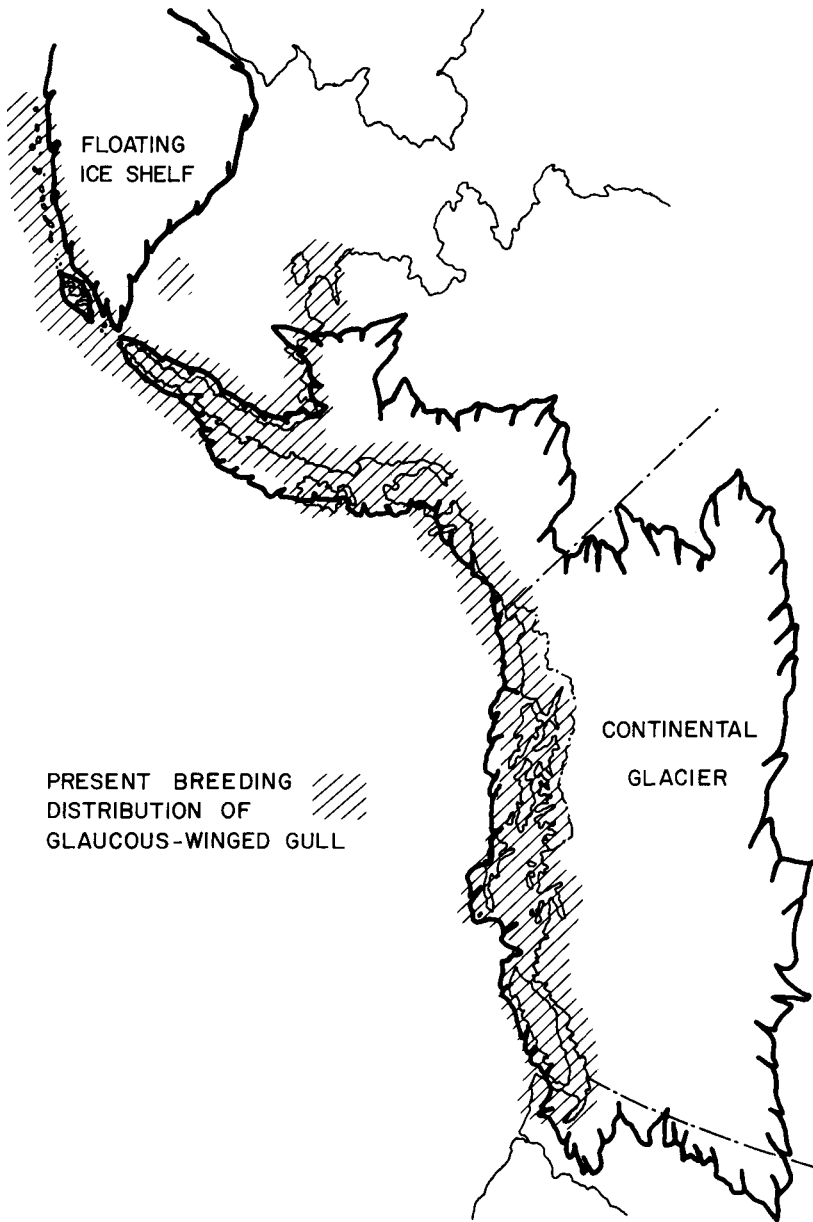
Fig. 6. The extent of major glaciation in western North America at the last Pleistocene maximum (ca. 12,000 years before present), with the present breeding distribution of Glaucous-winged Gulls superimposed (hatched zone).

Herring and Lesser Black-backed gulls (*L. fuscus*) are at least viable. Thus, considerable morphological differentiation has occurred without divergence of gene complexes to the extent that incompatibility results.

The adaptiveness of the color characters used in defining Glaucous-winged and Western gulls is far from clear. Smith (1966) reported that in the eastern Canadian Arctic these characters (pigmentation of the iris, eye-ring, and wing tips) were used

by gulls for species recognition. Harris' (1970) egg fostering experiments in *L. argentatus* and *L. fuscus* revealed a strong tendency for individuals (especially females) to chose mates similar to the birds that raised them. While the use of these characters in species recognition provides a selective force for maintaining distinctness in areas of sympatry, it does not explain the initial adaptiveness of the colors. Further, on the Oregon and Washington coasts the gulls do hybridize extensively, so the patterns are apparently not functioning as an effective barrier to mixed mating.

Within the *L. argentatus* species group, the mantle and wing tip colors of the adults show general latitudinal trends. The northernmost members of the group, *L. glaucoides* and *L. hyperboreus*, are very pale. They are replaced to the south by the pale-mantled, black-tipped Herring Gulls. Dark-mantled, black-tipped species (*L. marinus, L. fuscus, L. schistisagus, L. occidentalis*) live sympatrically with or to the south of the Herring Gulls. The most conspicuous anomaly in this general latitudinal gradient is the pale-winged *L. glaucescens* on the west coast of North America, with a range to the south of *L. argentatus*. Its present range closely corresponds to the extent of the glaciated coastline during the last Pleistocene maximum (Fig. 6). Possibly the Glaucous-winged Gull evolved in an environment (exposed headlands of glaciated landmasses) similar to the present habitat of the pale-winged *L. glaucoides*.

At the glacial maximum such habitat would have been restricted to a few suitable refugia. The Strait of Juan de Fuca was filled by a major glacial mass, and a floating ice-shelf may have extended along the southwest coast of Vancouver Island (Flint 1971), so there was probably a sizeable gap between the breeding ranges of the ancestral Glaucous-winged and Western gulls. Shortly after the glacial retreat from Puget Sound and coastal British Columbia the populations of Western and Glaucous-winged gulls should have completely colonized the intervening area. There is no reason to suppose that they have not been in contact continuously since then. Gaps of up to 60 km probably have existed (the Straits of Juan de Fuca, the Clatsop Plains of northern Oregon) within the present area of overlap, but these are clearly insufficient to isolate gulls. The first ornithological explorations of the Olympic Peninsula coast (Dawson 1909) demonstrated that hybridization was occurring before settlement of the area by Caucasians. The area apparently has been inhabited by American Indians for several thousand years, so recent human modification of the environment is not likely to be responsible for the contact or hybridization, as Sibley (1961) suggested for some hybridizing birds in the North American Great Plains.

If the contact between the populations is in fact old, the biological species concept would predict that the system should have evolved to or at least approached either complete reproductive isolation or completely random mating and clinal variation. Therefore we are led to examine the possibility that the expected selective pressures have not been present, and that the system has been maintained in its present intermediate form for some length of time. The hatching success data, taken together with the adult morphological data, indicate that postzygotic disadvantages to intergrades probably do not exist and that intermediates possess reproductive advantages. This reproductive advantage should drive the system to complete intergradation, with parental types not present in the zone of hybridization, even in the face of the level of assortative mating found at Destruction Island. The morphological analyses show that this has not happened. The simulation results demonstrate that low levels of immigration of parental types, taken together with the assortative mating patterns, can maintain parental types in considerable numbers.

At least two mechanisms can lead to this result. We lack sufficient evidence to

distinguish between them, or to eliminate other possible mechanisms, but they serve to demonstrate that the stability found in the simulation can be explained biologically.

If a consistent clinal variation exists in one or more environmental variables affecting fitness, so that pale (Glaucous-winged) gulls are favored to the north, dark-mantled (Western) gulls to the south, and intermediates in between, the system could potentially be stable in its present configuration. Moore (1977) favors such an explanation for the occurrance of most hybrid zones. In a continuously distributed population inhabiting such an environmental gradient a morphological cline should be expected. However, the gulls of the northwest coast are distributed discontinuously into discrete colonies, and gulls show a strong traditional tendency to return to and breed in their natal colony. If the environmental cline were very sharp, so that only a few colonies occupied the zone that was advantageous to intermediates, immigration could frustrate the development of a homogeneous intermediate population. Assortative mating could be a response of the well-adapted intermediates to restrict introgression from the locally less well-adapted parental types. The greatest weakness of this explanation is that the responsible environmental cline has not been identified, and in fact most of the climate-related possibilities are not monotonic in their variation through the region.

A rather different explanation is that there may not be *consistent* differences in average fitness between the Washington Glaucous-winged Gulls, the Oregon and southern Washington Western Gulls, and the intermediates, but that dispersal is not random with respect to fitness. Normally most gulls raised in a given colony will return to that colony to breed, but a sizeable minority can be found attempting to breed in other colonies or rarely at new sites. If the gulls that disperse are typically less fecund and/or less successful at caring for their eggs and young than those that breed in their natal colony, other gulls mating with them would have a selective disadvantage. If dispersal is a strategy employed by individuals that have been unsuccessful in gaining entrance to their natal colony, the dispersers as a class would be competitively inferior individuals. Dispersal may merely be a last chance effort to realize some reproductive output by individuals that are generalized "losers." Any variable population will continually be producing individuals of lower than average fitness, so the dispersal trait would be maintained. When habitat suitable for a new colony becomes available, dispersers would of course have a rare opportunity to realize high reproductive success.

Conspecific immigrants to a colony probably would be unrecognizable to the residents so a behavioral avoidance of these birds is unlikely. However, when a bird disperses to a colony of the other species, it potentially is recognizable as an immigrant, and therefore as a less fit mate. Thus, a degree of assortative mating should be present in the largely pure colonies. Numbers are of course small, but most of the Glaucous-winged Gulls found breeding at Yaquina Head, Oregon, were in pure pairs (Scott 1971). Within the mixed colonies, intergrade birds also would be more likely to avoid dispersers by mating preferentially with birds resembling themselves. There, as anywhere else, a bird of the most abundant type is most likely to get a superior mate by picking a bird like itself. The assortative mating pattern thus would be maintained. The higher frequency of immigrants in the pure pairs can account for the observed lower reproductive output. The nesting substrate preferences may serve to determine the location of the zone of overlap.

These two hypotheses for the maintenance of stability are not mutually exclusive.

They do demonstrate, however, that selective forces can exist to produce a stable zone of frequent hybridization with assortative mating.

TAXONOMY OF GLAUCOUS-WINGED AND WESTERN GULLS

The analyses of mating patterns and morphology clearly demonstrate that Short's (1969) and Mayr's (1969) criteria for conspecificity are not met. These criteria, in cases of population contact, essentially are that the zone of contact should be characterized by random mating, complete intergradation, absence of pure parental types, and introgression into the adjacent parental populations. Populations that meet and hybridize occasionally are referred to as semispecies. By these criteria, in their narrowest sense, Western and Glaucous-winged gulls should not be considered conspecific. Mating is not random, and parental types are present in numbers. However, the conclusion that the intermediate level of hybridization probably is persistent requires a reevaluation of the semispecies concept. Semispecies have been treated as allopatric members of superspecies, and as transient intermediate steps in cladogenesis. In fact, Mayr (1969:194) provided a listing of possible types of population contact that included zones of contact with occasional hybrids (semispecies) and zones of contact with complete intergradation or cline formation, but did not include intermediate conditions as a possibility. Thus the existence of partial reproductive isolation as a balanced condition extends the semispecies concept considerably. The role of coadapted gene complexes in speciation outlined by Mayr (1963, Ch. 17) is not operative here. This sort of semispecies overlap and hybridization zone occurs upon contact of populations that have fortuitously evolved partial behavioral isolating mechanisms without differentiating to the point of reduced hybrid fitness. These semispecies normally will not merge into a continuous population unless selection acts to break down the assortative mating systems, nor will they differentiate further toward full species until the selective regime changes to reduce fitness of intergrades.

The appropriate nomenclatural treatment for semispecies is to retain binomial distinction. The Western Gull of the Oregon and Washington coasts should remain *Larus occidentalis occidentalis* and the Glaucous-winged Gull, *L. glaucescens* (the proper nomenclatural treatment of the Glaucous-winged Gull is of course dependent upon the elucidation of its relationship with the Herring Gull in Alaska).

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