

# HYBRIDIZATION AND REPRODUCTIVE PERFORMANCE IN GULLS OF THE *LARUS GLAUDESCENS-occIDENTALIS* COMPLEX<sup>1</sup>

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**Abstract.** The Glaucous-winged Gull (*Larus glaucescens*) and the Western Gull (*L. occidentalis occidentalis*) hybridize along the Pacific Coast from Cape Flattery, Washington, south through central Oregon. A hybrid index, based on plumage and soft part colors, was used to study the distribution of morphotypes (e.g., pure and hybrid birds), mating patterns and reproductive performance at eight sympatric and two allopatric colonies. Mate choice appears to be weakly positive-assortative. In 1989 in the hybrid zone, *L. o. occidentalis* experienced significantly greater reproductive performance, measured as clutch size and egg volume difference, than either *L. glaucescens* or mixed pairs containing at least one hybrid individual. Although the hybrid zone has expanded somewhat in recent times, the midpoint of the zone and the relative proportion of morphotypes has remained stable. The hybrid zone is situated on a marine-ecotone. Within the hybrid zone, relative reproductive performance of *L. o. occidentalis* and hybrids may shift between years, whereas *L. glaucescens* may experience poor reproductive performance in all years. The selection-hybridization balance hypothesis may best explain the *L. glaucescens-occidentalis* hybrid zone.

**Key words:** gulls, hybridization, *Larus glaucescens*, *Larus occidentalis*, reproductive fitness, selection-hybridization balance.

## INTRODUCTION

Neo-Darwinism traditionally has used examples of hybridization to test hypotheses related to speciation (e.g., Bush 1975). Now the emphasis is shifting away from viewing hybridization as simply a measure of speciation to a focus on the process itself (Barton and Hewitt 1989, Harrison 1993). For example, although the concept of gene exchange or introgression between species is not new (Anderson and Hubricht 1938), recent study of avian hybrid zones reveals that hybridization also may function as a creative force to increase genetic diversity without breaking down species barriers, especially in those forms adapted to local environments (Grant and Grant 1992, Moore and Price 1993, Parsons et al. 1993). Indeed, Panov (1989) has proposed that hybridization in birds represents an evolutionary response to fluctuating environmental conditions. Contact zones thus offer opportunities to re-evaluate evolutionary processes at the individual, population and species level.

In the eastern Pacific, the Glaucous-winged Gull *Larus glaucescens* breeds from the Gulf of

Alaska south through coastal British Columbia and Washington to Oregon (AOU 1983). The northern race of the Western Gull *L. occidentalis occidentalis* breeds from islands in Juan de Fuca Strait and the outer Washington coast south to Monterey Bay in central California (AOU 1983). These two species hybridize where their ranges overlap along the Washington and Oregon coastlines. Interbreeding between *L. glaucescens* and *L. o. occidentalis* was first noted by Dawson (1908). Since then, miscellaneous reports of hybridization have been published (Pearse 1946, Weber 1981) and surveys of the hybrid zone have been undertaken (Scott 1971, Hoffman et al. 1978). Bell (1996) presented results from an extensive study of morphometric and protein electrophoretic variation in this complex of gulls, and Hoffman et al. (1978) investigated the dynamics of this hybrid zone incorporating data on mating patterns and reproductive success.

Using methods comparable to those of Hoffman et al. (1978), this paper presents information on the distribution of morphotypes, mate choice, and reproductive performance in the *L. glaucescens-occidentalis* complex. Most of the data for this study were collected in 1989. Hoffman et al. (1978) collected their reproductive success data in 1974. Thus, changes in the hybrid zone that may have occurred in the inter-

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vening 15 years are discussed, and hybridization between *L. glaucescens* and *L. o. occidentalis* is evaluated in light of two hypotheses that have been proposed to explain hybrid zones: bounded hybrid superiority (Moore and Buchanan 1985, Moore and Price 1993) and selection-hybridization balance (Grant and Grant 1992, 1993). Both hypotheses concern the differential effect of selection on hybrids and parentals in the ecotonal condition of the hybrid zone. Under bounded hybrid superiority, a stable hybrid zone persists because hybrids are more fit than parentals in the hybrid zone (Moore and Buchanan 1985, Moore and Price 1993). Under selection-hybridization balance, ecotonal conditions in the hybrid zone fluctuate in such a way that hybrids are more fit than parentals in some years and less fit in other years, a situation that may result in a balance between bouts of hybridization followed by periods of selection against hybrids (Grant and Grant 1992, 1993). Although the results from Hoffman et al. (1978) are consistent with the bounded hybrid superiority hypothesis, additional data presented here suggest that the *L. glaucescens-occidentalis* hybrid zone is perhaps more consistent with the selection-hybridization balance hypothesis.

## METHODS

Study sites were selected to establish two reference colonies of presumptively pure taxa outside of the hybrid zone (Langara Island, British Columbia, for pure *L. glaucescens*, and Alcatraz Island, California, for pure *L. o. occidentalis*) and eight colonies of mixed composition in Oregon and Washington located within the hybrid zone (Fig. 1, Table 1). Most colonies were visited during the incubation phase of the nesting cycle. Observation tents were set up in each colony, and all gull nests visible from the tent were marked and numbered with pvc or wooden stakes. Each nest was watched until mate exchanges occurred, permitting each member of a pair to be scored with a hybrid index (see below) and sexed. Males were differentiated from females on the basis of their larger overall body size, more substantial heads and larger bills, and in some cases, overt sexual behaviors (Verbeek 1993, Pierotti and Annett 1995). Most observations were made through a 10–40× zoom spotting scope during mid-day hours when ambient lighting conditions were optimal. Nest contents, e.g., clutch size, was recorded during visits, and

each egg of a clutch was numbered, weighed to the nearest gram, and measured in length and breadth. A total of 475 pairs out of 966 individual gulls across the 10 colonies was scored with the hybrid index.

Adult *L. glaucescens* have light gray mantles (backs) and subterminal primary feather tips (primary tips), pink legs, and a straw-yellow bill. The ground color of the iris is light gray, but this is usually partially masked by blotchy dark brown pigment. The eye is surrounded by a deep pink or vinaceous orbital ring (= eye-ring). Adult *L. o. occidentalis* have a dark gray mantle and nearly black primary tips, pink legs and feet, and a straw-yellow to orange-yellow bill. The iris is straw-yellow with slight brownish flecking usually distributed over the lower third of the iris. The eye is surrounded by a yellow to orange-yellow eye-ring.

A hybrid index (HI), similar to that of Hoffman et al. (1978), was devised to identify gulls to putative morphotype (e.g., pure or intergrade) in the field and to detect changes in the hybrid zone since 1974. The use of an HI is an effective method of identifying birds in the field (Moore and Koenig 1986). In addition, HI scores are highly reproducible (Corbin and Barrowclough 1977). The HI consisted of the sum of individual scores for mantle color, primary tip pigmentation, eye-ring color, dark brown iris pigmentation, and iris color (Table 2), and was set up so that pure *L. o. occidentalis* would have low scores and pure *L. glaucescens* would have high scores. Mantle shading and primary tip pigmentation were scored by matching these plumage characters to a Munsell 37-step neutral value scale (Munsell 1971). Mantle grayness was scored on a scale of 0 to 7, encompassing a range of Munsell neutral values from  $N = 3.25$  (= dark gray) to  $N = 7.00$  (light gray). Primary tip pigmentation was scored on a scale of 0 to 10, spanning Munsell neutral values from  $N = 1.00$  (black) to  $N = 6.25$  (light gray). In the field, the hand held gray scale chart was oriented towards incident light at the same angle as the gull under observation. Eye-ring pigment was scored from 0 to 4; with yellow/orange yellow = 0, yellow/flesh = 1, pink/yellow = 2, pink/flesh = 3, and pink = 4, whereas intensity of the eye-ring pigment was scored 0 (light/medium) or 1 (dark). Iris pigment received three scores based on the intensity of the brownish pigment (light = 0, medium = 1, and dark =

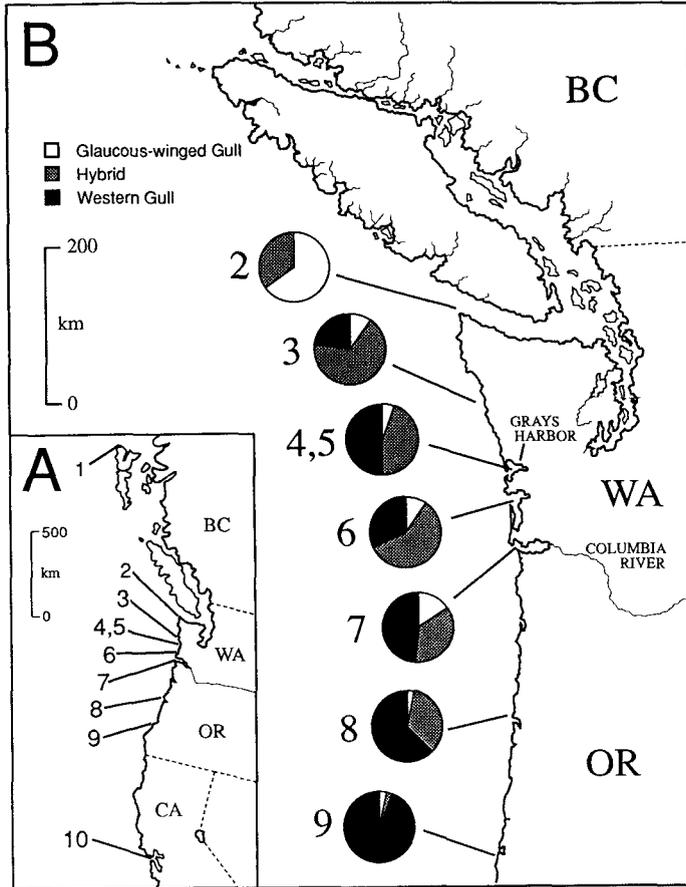


FIGURE 1. A. Locations of 10 colonies sampled in this study. Table 1 lists exact locations and names of each colony. Note that colony 1 is pure *L. glaucescens*, colony 10 is pure *L. o. occidentalis*, and colonies 2–9 are in the hybrid zone. B. Map of the hybrid zone. Pie diagrams illustrate the relative proportion of *L. glaucescens*, hybrids, and *L. o. occidentalis* present at each colony as determined by the hybrid index (HI). Data are pooled for colonies 4 and 5, located in Grays Harbor, Washington.

2), form of the pigment (even = 0, grainy/blotchy = 1), and the proportion of pigment covering the iris ( $\leq 25\%$  = 0;  $\leq 50\%$  = 1;  $\leq 75\%$  = 2;  $\leq 100\%$  = 3). Iris ground color was noted as either yellow/yellow-green (= 0) or gray (= 1), the latter score of which applied to many gulls of the *glaucescens* morphotype.

Hoffman et al. (1978) did not standardize their HI, hence, their HI weighted characters differentially, especially plumage. In order to directly compare my results with those of Hoffman et al. (1978), I did not standardize my HI either. Thus, the results presented here are biased towards plumage-based determinations of morphotype.

To test whether mating between gulls was

nonrandom with respect to the HI, intrapair Pearson  $r$  was calculated, combining all colonies in the hybrid zone (colonies 2–9; Fig. 1). Individual HI's were adjusted prior to analysis to account for colony differences by subtracting the sex-specific colony mean HI from the individual HI. This adjustment accounted for intercolony differences in the pool of available mate types.

To evaluate taxon-specific reproductive success, birds were classified into three categories, *L. occidentalis occidentalis* (WN), hybrid (HY), and *L. glaucescens* (GW), based on their HI score (see below). Data on reproductive performance were acquired during the spring of 1989. To measure reproductive performance, clutch size and egg volume difference were determined

TABLE 1. Gull colony locations, sample sizes, and dates visited. Colony numbers correspond to those in Figure 1. In some locations, more individuals than mated pairs were categorized with the hybrid index. Abbreviations: WN = Western Gull, HY = hybrid gull, GW = Glaucous-winged Gull.

Colony No.	Colony location	No. pairs	No. individuals			Dates of colony visits
			GW	HY	WN	
1.	Langara I., Queen Charlotte Is., BC	16	32	0	0	12-13 June 1990
2.	Tatoosh Island, WA	99	129	69	0	19-23 June 1989 24-27 June 1990
3.	Destruction Island, WA	69	12	97	29	24-28 June 1989
4.	Sand I., Grays Harbor, WA	36	3	30	39	13-14 June 1989
5.	Whitcomb I., Grays Harbor, WA	52	8	47	49	15-16 June 1989
6.	Pine I., Willapa Bay, WA	54	10	63	35	8-9 June 1989
7.	East Sand I., Columbia River, OR	78	24	52	80	23-29 May 1989 10-12 June 1989
8.	Yaquina Head, OR	14	1	11	20	2-3 June 1989
9.	Gregory Point, Cape Arago, OR	20	1	1	43	31 May-1 June 1989
10.	Alcatraz I., S. F. Bay, CA	30	0	1	59	16 May, 1 June 1990
Total		468	220	371	354	

for the various pairing combinations. In gulls that lay a three-egg clutch, the third egg is typically smaller than the first two (Parsons 1972). The smaller size of the third egg, relative to the size of the first two eggs, is correlated with a host of factors such as hatching asynchrony, lower hatching success, and reduced chick survivorship, otherwise known as the "third chick disadvantage" (Pierotti and Bellrose 1986, Reid 1987). Given that the third-chick disadvantage is associated with small egg size, and that small third eggs may be a facultative response to food supply or energy reserves (Pierotti and Bellrose 1986, Sydeman and Emslie 1992), it can be assumed that among gulls with three-egg clutches those with the least difference in volume between the third egg and the first two eggs will

have greater reproductive success (see also Kilpi 1995). Egg volumes were derived from width and breadth measurements (mm) using the formula of Hoyt (1979), and egg volume difference was calculated as the difference in volume between the average of the first two eggs and the smaller third egg in three-egg clutches. One-way ANOVA was used to test for significant variation in clutch size and egg volume difference among pairs consisting of pure *L. o. occidentalis* (WN × WN), pure *L. glaucescens* (GW × GW), and mixed pairs, that is, a pairing combination where at least one member of the pair is a hybrid. The mixed pair category did not include reciprocal crosses between pure WN and GW gulls. Small sample sizes precluded using these reciprocal crosses in the ANOVA.

TABLE 2. Character score (CS) given to different components of the hybrid index (HI). The character scores were summed to provide an HI. HI sums ranged from 0-29 and were classified Western Gull (0-8), hybrid (9-19), and Glaucous-winged Gull (20-29).

Mantle		Primary Tips		Eye-ring		Iris pigment		Iris color	
Munsell:	CS	Munsell:	CS	Color:	CS	Intensity:	CS	Color:	
3.25-3.50	0	1.00-1.25	0	Yellow-orange	0	Light	0	Straw Yellow	0
3.75-4.00	1	1.50-1.75	1	Yellow-flesh	1	Medium	1	Gray	1
4.25-4.50	2	2.00-2.25	2	Pink/Yellow	2	Dark	2		
4.75-5.00	3	2.50-2.75	3	Pink-flesh	3	Form:			
5.25-5.50	4	3.00-3.25	4	Pink	4	Even/diffuse	0		
5.75-6.00	5	3.50-3.75	5	Intensity:		Grainy/blotchy	1		
6.25-6.50	6	4.00-4.25	6	Light/medium	0	Distribution:			
6.75-7.00	7	4.50-4.75	7	Dark	1	≤25%	0		
		5.00-5.25	8			≤50%	1		
		5.50-5.75	9			≤75%	2		
		6.00-6.25	10			≤100%	3		

## RESULTS

The distributions of male and female HI scores within each colony did not differ (Kolmogorov-Smirnov tests;  $D$  ranged from 0.083 to 0.312;  $P$  ranged from 0.27 to 0.99), therefore, HI scores for both sexes were combined. HI scores were highest at colony 1 (range 21–28), Langara Island, British Columbia, and lowest at colony 10 (range 0–6), Alcatraz Island, California (Fig. 2). These two colonies represent allopatric populations of *L. glaucescens* and *L. o. occidentalis*, respectively. Due to clinal variation in mantle and primary tip coloration (Bell 1992, 1996), presumptive *L. o. occidentalis* from Oregon and Washington can have an HI score as high as 8, while *L. glaucescens* from the same region may score as low as 20. Therefore, gulls with HI scores from 0 to 8 were classified as putative *L. o. occidentalis*, those scoring from 20 to 28 were designated *L. glaucescens*, and those with HI scores ranging from 9 to 19 were classified as putative hybrids.

Sympatric colonies 2–9 exhibit ranges of HI scores that include extreme high and low values (Figs. 1 and 2). Note that the HI distribution varies with location (Fig. 2): there is a marked shift from *L. glaucescens* and *glaucescens*-like gulls at Tatoosh Island, Washington (colony 2) to *L. o. occidentalis* and *occidentalis*-like individuals at Destruction Island, Washington (colony 3). These two islands are only 90 km apart along the outer Washington coast, but their HI distributions are approximate mirror images. The HI distributions of Colonies 3 to 7 are similar and delineate a region of maximum sympatry. This region spans approximately 180 km of the outer Washington coast from Destruction Island south to the mouth of the Columbia River. Note that although colonies 3 to 7 correspond to a region of maximum overlap between *L. o. occidentalis* and *L. glaucescens*, the latter comprises only about 10% of the total gull population in this region (Table 1). Two colonies had more than 50% hybrids: Destruction Island and Willapa Bay (Table 1, Fig. 2). The mid-point of the hybrid zone is centered around Grays Harbor, Washington. A single adult male hybrid gull was present on Alcatraz Island (colony 10) in San Francisco Bay, California.

A plot of intrapair adjusted male hybrid index (MHI) versus adjusted female hybrid index (FHI) for combined hybrid zone colonies 2–9

yielded a significant correlation ( $r = 0.28$ ,  $P < 0.001$ ; Fig. 3), suggesting that gulls within the *L. glaucescens-occidentalis* complex mate non-randomly with respect to the HI, and that mate choice is positively assortative, albeit weakly.

Mean clutch size was largest in pure *L. o. occidentalis* (WN) pairs, smallest in pure *L. glaucescens* (GW), and intermediate in mixed pairs, i.e., pairs containing at least one hybrid gull (Table 3). Variation in clutch size between WN, mixed, and GW pairs was greater than expected by chance ( $F_{2, 302} = 4.09$ ,  $P < 0.02$ ). The difference in volume between the average of the first two eggs and the third egg in three-egg clutches also varied more than expected by chance among pure and mixed pairs (Table 3,  $F_{2, 145} = 3.16$ ,  $P < 0.05$ ). Egg volume difference in mixed pairs was intermediate between the values for pure pairs, and among pure pairs, GW pairs showed the largest difference in egg volume (Table 3). Taken together, these data suggest that in 1989, *L. o. occidentalis* pairs experienced greater reproductive performance in the hybrid zone than mixed pairs, which in turn, experienced greater reproductive performance than *L. glaucescens* pairs.

## DISCUSSION

### ASSORTATIVE MATING

The present study is consistent with earlier work by Hoffman et al. (1978) suggesting that sympatric members of the *Larus glaucescens-occidentalis* complex mate assortatively. The distribution of HI scores in the hybrid zone (Fig. 2) implies that most backcrossing involves intergrade gulls that are close in phenotype to pure parentals. Bell (1992) found that of 289 mated pairs categorized to morphotype in colonies 3 to 7 (Fig. 1), only 16 involved crosses between pure *L. glaucescens* and *L. o. occidentalis*. Thus, less than 6% of the total crosses in the region of maximum sympatry would be expected to produce  $F_1$  hybrids. The general lack of *L. glaucescens* in this region of the hybrid zone undoubtedly contributes to the low level of reciprocal crossing.

Assortative mating implies that the members of a pair are basing their choice on some phenotypical or behavioral character, or a combination thereof. Several different characters have been posited as functioning in the specific mate recognition system of larids, including eye-ring color (Macpherson 1961), the amount of contrast between the eye and the white head (Smith

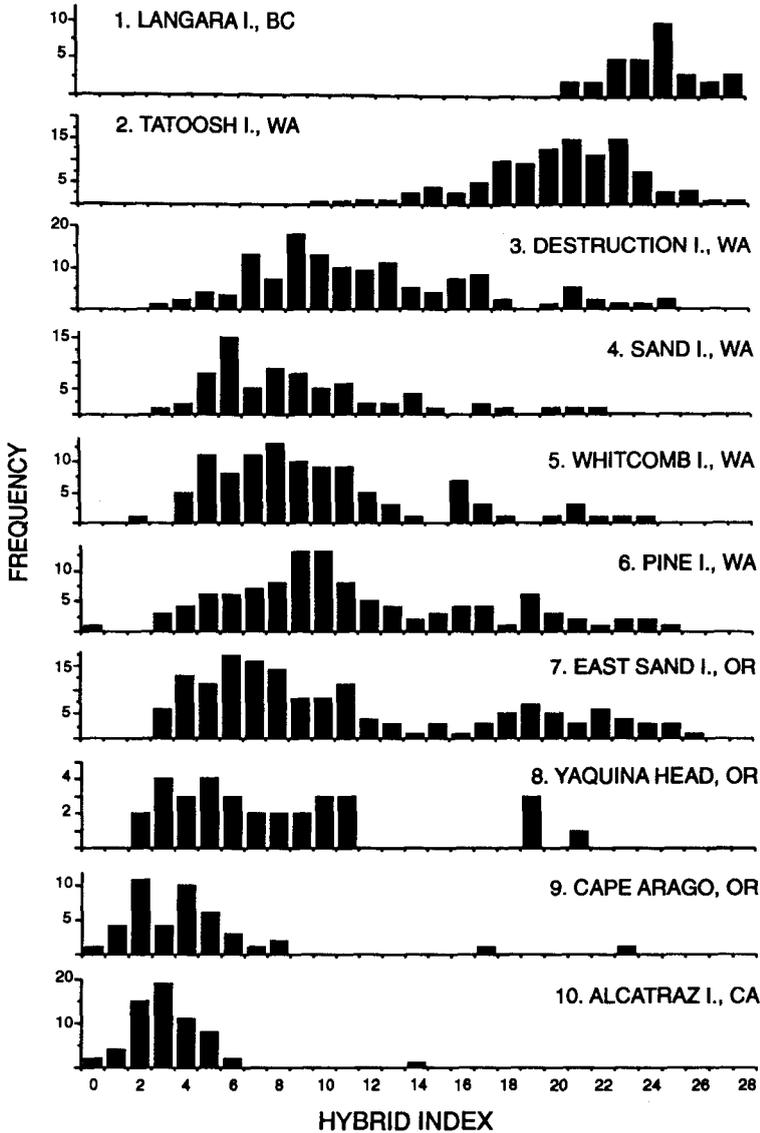


FIGURE 2. Frequency distribution of hybrid index scores in each of the 10 colonies where breeding gulls were identified with the hybrid index. Refer to Figure 1 for map of colony locations.

1966, but see Snell 1991), and the color of the bill and foot (Pierotti 1987). Although their relative efficacy as specific isolators appears to be low, the plumage and soft part colors investigated here, as expressed by the HI, appear to contribute to mate choice in the *L. glaucescens-occidentalis* complex.

RELATIVE FITNESS

Two independent measures of reproductive performance, clutch size and egg volume differ-

ence, revealed significant differences among gull morphotypes in 1989. *Larus o. occidentalis* pairs (WN × WN) experienced greater reproductive performance than mixed pairs, which in turn exhibited greater reproductive performance than *L. glaucescens* pairs (GW × GW). This is in contradistinction to the results of Hoffman et al. (1978), who in 1974 noted that mixed pairs containing at least one hybrid individual had significantly higher reproductive success than pure pairs. Their measure of reproductive success,

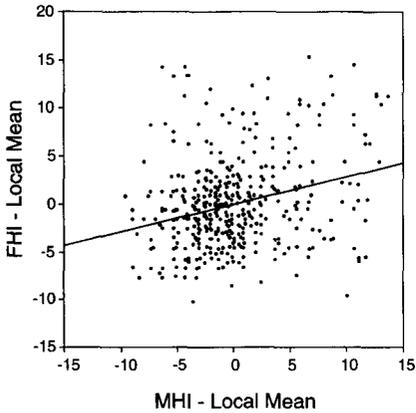


FIGURE 3. Matrix of mating preferences based on the adjusted hybrid index to account for differences in location: male hybrid index (MHI)—local mean vs. female hybrid index (FHI)—local mean; for 422 mated pairs categorized by HI in the hybrid zone colonies 2 to 9 (Fig. 1). The solid line represents the correlation ( $r = 0.28$ ,  $P < 0.001$ ).

based on hatching success, did not differ in overall trend from their clutch size data (Hoffman et al. 1978). Thus, assuming the measures obtained in both studies are comparable, it appears that the pattern of reproductive fitness in the hybrid zone shifted: in 1974 hybrids experienced greater reproductive fitness than parentals; in 1989 *L. o. occidentalis* fared better than either hybrids or *L. glaucescens*. In both study years *L. glaucescens* pairs experienced the poorest reproductive success.

Reasons for the apparent shift in reproductive fitness in the hybrid zone in 1974 versus 1989 are entirely unknown. The *L. glaucescens-occidentalis* hybrid zone appears to be positioned on an interface, or ecotone (*sensu* Remington 1968), between an upwelling and non-upwelling marine environment. North of this ecotone, *L.*

*glaucescens* is the predominant breeding gull, inhabiting a marine environment characterized by the complex fjord, bay and estuarine circulation patterns of Puget Sound and British Columbia (Thomson 1981). South of the ecotone, where the California Current and associated wind-induced upwelling characterizes the marine environment in spring and early summer (Huyer 1983), *L. o. occidentalis* is the only breeding gull of the *glaucescens-occidentalis* complex. The latitude at which the California Current strikes the Pacific Northwest coast varies, and the current itself exhibits interannual variation in strength (Thomson 1981, Huyer 1983), therefore, the exact width of the ecotone, or transition zone, between the upwelling and non-upwelling marine environment along the Pacific Northwest coast may be expected to vary, too. Thus, interannual variation in the uncertain marine and coastal environments of the ecotone could be responsible for shifts in reproductive performance between pure and hybrid gulls.

Environmental factors that influence larid productivity in general, and those that might influence the extent of the ecotone, in particular, could be posited as possible explanations for shifting reproductive fitness in the hybrid zone. For instance, in the eastern Pacific, the rise in sea surface temperatures and sea levels associated with El Niño-like phenomena suppresses the upwelling of nutrients, causing a decrease in ocean productivity that ultimately affects seabird populations by lowering breeding success and increasing mortality (Schreiber and Schreiber 1984, Ainley 1990). In *L. glaucescens*, Murphy et al. (1984) found a general correlation between increased reliance on invertebrate prey and decreased reproductive performance, and Paine (1986) noted that gulls nesting on Tatoosh Island

TABLE 3. Mean clutch size and egg volume difference for pairing combinations in the *L. glaucescens-occidentalis* complex, where WN = Western Gull, GW = Glaucous-winged Gull, and MIXED refers to any pair combination containing at least one hybrid gull. Data are from hybrid zone colonies 2-9 (see Table 1, Fig. 1).

Pair type Male × Female	Clutch size		Volume difference	
	$\bar{x} \pm SD$	<i>n</i>	$\bar{x} \pm SD$	<i>n</i>
WN × WN	2.57 ± 0.90*	65	4.80 ± 3.70*	45
GW × WN	2.29 ± 1.11	7	4.72 ± 2.88	4
WN × GW	2.25 ± 1.30	8	2.56 ± 3.20	4
MIXED	2.18 ± 1.02*	214	6.57 ± 4.40*	91
GW × GW	2.08 ± 1.29*	26	7.33 ± 5.04*	12

\* One-way ANOVAs between WN × WN, GW × GW and MIXED pairs showed clutch size and egg volume difference vary significantly (see text).

off Cape Flattery in the Pacific Northwest experienced reduced fecundity one year after the major 1982–1983 El Niño event, apparently because they relied more heavily on invertebrate prey than in other years. I speculate that in years when the ecotone is maximally expanded, hybrids will experience greater reproductive performance than *L. o. occidentalis*. In other years, when the ecotone is reduced to a minimum, *L. o. occidentalis* may experience greater reproductive performance. In all years, *Larus glaucescens* experiences poor reproductive success in the southern reaches of the hybrid zone because it is at the limit of its spring and summer ecological range.

The foregoing considers only limited indicators of reproductive success. Good et al. (1996) found that type of nesting habitat in hybrid colonies in Grays Harbor influences egg survivability. Hence, differential hatching success among morphotypes in different nesting habitats in the hybrid zone could alter the relative reproductive fitnesses measured here. Likewise, juvenile and adult mortality rates could reverse or accentuate trends in overall relative fitness between hybrids and parentals. For instance, in the *L. argentatus-hyperboreus* hybrid zone of Iceland, Ingolfsson (1987) found that *argentatus*-like gulls experienced lower reproductive success than other morphotypes, whereas *hyperboreus*-like birds had lower mortality rates. Thus, determining the overall fitness of each morphotype in the *L. glaucescens-occidentalis* complex must await additional data on life history parameters and environmental perturbations in the hybrid zone.

#### CHANGES IN THE HYBRID ZONE

The hybrid zone has expanded moderately since 1974 (compare Hoffman et al. 1978:444, this study). Specifically, the relative proportion of hybrids at colonies in the northern and southern ends of the zone has increased, and both *L. glaucescens* and *L. o. occidentalis* have undergone breeding range expansions (Bell 1996). The overall increase in the incidence of hybridization may be due in part to the expansion of gull populations in the Pacific Northwest over the latter half of this century (Campbell et al. 1990). Nevertheless, some elements of the hybrid zone appear to be stable. The midpoint of the hybrid zone, located near Grays Harbor, Washington, has not shifted since mixed colonies of the two

species were first reported by Dawson (1908). The main region of sympatric overlap still consists of an approximately 180-km stretch of the outer Washington coast, and the relative proportion of morphotypes at most colonies within this region has remained constant. Pure parentals are found at colonies throughout the hybrid zone, and as a species, putatively pure *L. glaucescens* appears to exhibit isolation by distance as if it were at equilibrium under dispersal and genetic drift (Slatkin 1993). In sum, it appears that a hybrid swarm is not developing, and that the hybrid zone is in fact relatively stable despite some recent expansion.

#### HYBRID ZONE HYPOTHESES

Hoffman et al. (1978) modeled the population dynamics of the *L. glaucescens-occidentalis* hybrid zone using the reproductive success data they collected on Destruction Island in 1974. They used various life history parameters to simulate a stable hybrid zone and found that the greater reproductive success of mixed pairs containing at least one hybrid could be countered by a low level of immigration of pure parentals into the region of sympatry. These data would suggest that the *L. glaucescens-occidentalis* hybrid zone might best be explained by the bounded hybrid superiority model (Moore and Buchanan 1985, Moore and Price 1993). Under this hypothesis, a stable hybrid zone persists in an ecotone between the ranges of the parental species despite extensive interbreeding because the parental phenotypes are less fit than hybrids in the zone of overlap. However, the present study suggests that interannual variation in relative fitness may shift between morphotypes. As a working hypothesis, I suggest that the *L. glaucescens-occidentalis* hybrid zone is best explained by a selection-hybridization balance (Grant and Grant 1992, 1993). Under this hypothesis, hybrids would be expected to experience greater reproductive fitness in some years, whereas in other years, *L. o. occidentalis* will experience greater fitness. Because relative fitness within the zone fluctuates from year to year, complete swamping of parentals or complete elimination of hybrids cannot occur. Such a situation should proceed indefinitely, as appears to be the case for some hybridizing species of Darwin's finches in the Galapagos Islands (Grant and Grant 1992). Furthermore, *Larus glaucescens* will not be able to penetrate the hybrid

zone to any great degree because it is not adapted to the upwelling conditions of the California Current and, except for some coastal bays, the coastline south of the Columbia River does not provide the extensive inland waterway and estuarine habitat preferred by this species. I hypothesize that the selection-hybridization balance permits *L. glaucescens* and *L. o. occidentalis* to hybridize in waxing and waning pulses that, although favoring introgression directed towards *L. glaucescens* (Bell 1996), may not lead to swamping of either species.

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