

BOUNDED HYBRID SUPERIORITY IN AN AVIAN HYBRID ZONE: EFFECTS OF MATE, DIET, AND HABITAT CHOICE

THOMAS P. GOOD,¹ JULIE C. ELLIS,¹ CYNTHIA A. ANNETT,² AND RAYMOND PIEROTTI³

Division of Biological Sciences, University of Kansas, Lawrence, Kansas 66045-2106

³*E-mail: pierotti@falcon.cc.ukans.edu*

Abstract.—There has been considerable debate in the study of hybrid zones as to whether hybrids may be superior to parental types within the area of contact (bounded hybrid superiority). In birds, naturally occurring hybridization is relatively common, and hybridization within this group always involves mate choice. If hybrids are superior, females choosing heterospecific mates should be expected to show higher fitness under the conditions prevalent in the hybrid zone. Hybrid superiority under these circumstances would reduce reinforcement and thereby help to maintain the hybrid zone. To examine this issue, we studied reproductive performances of hybrids and parental species of gulls (*Larus occidentalis* and *Larus glaucescens*) at two colonies within a linear hybrid zone along the west coast of the United States. This hybrid zone contains predominantly gulls of intermediate phenotype. Previous studies indicated that hybrids were superior to one or both parental types, but provided no data on possible mechanisms that underlie this hybrid superiority. Using a hybrid index designed specifically for these species, we identified to phenotype more than 300 individuals associated with nests, including both individual males and females within 73 pairs in the central portion of the hybrid zone and 74 pairs in the northern portion of the hybrid zone. There was little evidence of assortative mating, and what little there was resulted solely because of pairings within intergrades. In the central hybrid zone, females paired with hybrid males produced larger clutches and hatched and fledged more chicks compared with females paired to western gull males. This was a result of heavy predation on eggs in sand habitat, where male western gulls established territories. In contrast, many hybrid males established territories in vegetated cover that was less vulnerable to predation. In the northern part of the hybrid zone, clutch size did not differ among pair categories, however, there were differences in hatching and fledging success, with females paired to hybrid males showing better success compared to females paired to glaucous-winged gull males. Hybrids showed better hatching and fledging success in the north because hybrids are more like western gulls than glaucous-winged gulls in foraging behavior, taking a higher percentage of fish in their diet, which enhances chick growth and survival. This is believed to be the first documentation of bounded hybrid superiority that delineates the mechanisms that underlie hybrid superiority.

Key words.—Birds, gulls, hybrid superiority, hybrid zone, *Larus*, mate choice.

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Hybrid zones resulting from secondary contact between two taxa often form in ecotones (Moore 1977; Barton and Hewitt 1985; Hewitt 1988). Within hybrid zones, it is possible that hybrids are selectively favored because they are better adapted to conditions within the ecotone than the parental forms, a situation referred to as geographically “bounded hybrid superiority.” (Moore 1977; Moore and Price 1993). Although the theoretical basis of this argument is well developed, empirical demonstrations of bounded hybrid superiority are rare in the literature, and those that exist consist of demonstrations either that hybrid zones have persisted over a long period of time (Moore and Buchanan 1985) or that reproductive performance of hybrids is at least equivalent to that of parental types (Moore and Koenig 1986; Saino and Villa 1992). In those few situations where bounded hybrid superiority has been invoked, mechanisms that generate the superiority of hybrids have not been demonstrated (Grant and Grant 1992, 1997a,b; Moore and Price 1993).

If hybrids actually are superior in fitness to parental types, choosing a heterospecific as a mate should incur no fitness costs and could even be selectively favored, if the heterospecific male is of superior quality (Pierotti and Annett 1993). Thus, empirical studies of hybridization as a process should involve investigation of patterns of mate choice, because all

hybridization events in birds involve active choice of a mate and because under conditions of bounded hybrid superiority, the frequency of hybridization should result directly from patterns of mate choice (Pierotti and Annett 1993; Grant and Grant 1997a,b).

Intensive investigations within hybrid zones are necessary to understand their evolutionary history, and may increase our understanding of speciation (Hoffman et al. 1978). Hybridization has been found in more than 10% of known avian species (Panov 1989; Grant and Grant 1992; Pierotti and Annett 1993), and most major examples of hybrid superiority are known from birds (Moore and Buchanan 1985; Moore and Koenig 1986; Grant and Grant 1992; Saino and Villa 1992). We therefore focused our research on the mechanisms leading to bounded hybrid superiority on an avian hybrid zone.

Hybridization in Larus Gulls

We chose gulls of the genus *Larus* for our study of the relationship between mate choice and reproductive success in hybrid zones because gulls are socially monogamous birds that show mate choice by both sexes combined with extensive male parental care (Burger 1981; Pierotti 1981, 1987a; Morris 1987). Male gulls establish the location of the breeding territory within specific habitat types and provide the bulk of food for females during egg formation and during chick rearing (Burger 1981; Pierotti 1981, 1987a). Female choice appears to be based initially on quality of nesting territory,

¹ Present address: Department of Ecology and Evolutionary Biology, Brown University, Providence, Rhode Island 02912.

² Present address: Haskell Environmental Research Studies Center, Haskell Indian Nations University, Lawrence, Kansas 66046.

which can have a major impact on reproductive performance, especially if the habitat provides shelter from agonistic behavior and predation (Pierotti 1982, 1987a). Mate choice is reinforced by the rate and quality of food provided by the male, in that reproductive performance suffers and the female may desert the nest if adequate food is not provided (Pierotti 1987a; Pierotti and Annett 1987, 1990; Annett and Pierotti 1999). *Larus* gulls also show a strong tendency toward hybridization in nature, with 22 of 42 recognized species known to hybridize (Pierotti 1987b; Panov 1989). Gulls appear to be free of postzygotic barriers to hybridization, presumably because they show relatively low genetic differences between taxa (Avise 1983; Shields 1987; Snell 1991).

The best studied gull hybrid zone occurs along coastal Oregon and Washington, at the southern range limit of the glaucous-winged gull, *L. glaucescens*, and the northern range limit of the western gull, *L. occidentalis* (Dawson 1909; Pearse 1946; Scott 1971; Hoffman et al. 1978; Bell 1992; Good 1998). These taxa do not appear to be closely related (Chu 1998); therefore, reproductive isolation should be well developed. Preliminary studies in the western/glaucous-winged gull hybrid zone suggested that pairs containing hybrid individuals showed higher hatching success (Hoffman et al. 1978) or that pairs containing hybrids produced both eggs and clutch sizes smaller than those of pure western gull pairs, but larger than those of pure glaucous-winged gull pairs (Bell 1992, 1996). Neither of these studies, however, compared the performance of females paired with heterospecifics to females paired with conspecifics, nor did they provide data on possible mechanisms to explain why hybrids should be superior to parental types.

METHODS

Study Sites

Hybridization was originally reported between western and glaucous-winged gulls along the Olympic Peninsula at the beginning of the century (Dawson 1909). The first detailed description of the hybrid zone was provided by Scott (1971), who described the zone of intensive hybridization as occurring in a 180-km stretch of coast from the Columbia River north to Alexander Island, just south of the Quilleute Village of La Push. Subsequent work by Bell (1992) indicated that the zone of intensive hybridization had extended as far as Cape Flattery by the late 1980s. We initiated a study of the nesting habitat preferences and diet choice within this zone of intensive hybridization in May 1994. Data were collected at two major populations within the area described as being the primary hybrid zone (Fig. 1): Gray's Harbor, Washington, located in the central part of the hybrid zone (46°57'N 124°03'W), where breeding individuals are almost exclusively western gulls and hybrids, and Tatoosh Island, adjacent to Cape Flattery in the northern part of the hybrid zone (48°23'32''N 124°44'07''W), where breeding individuals are almost exclusively glaucous-winged gulls and hybrids (Bell 1992).

Data were collected in Gray's Harbor during 1994–1996 (Good 1998). We examined gulls nesting on Sand Island (46°57'45''N 124°03'25''W), an unnamed new island (46°57'30''N 124°03'05''W) in the northern part of the bay,

and Whitcomb Flats (46°54'40''N 124°04'40''W) in the southern part of the bay (Fig. 1). Data were collected on Tatoosh Island during 1996–1997.

Assessment of Reproductive Performance and Diet

We examined patterns of pairing and reproductive performance within the hybrid zone by comparing breeding performance at nests where one or both members of the breeding pair could be clearly identified. Pairs were classified as hybrid if (1) the only identified individual found associated with a nest was classified as a hybrid; or (2) at least one of the two members of the pair was a hybrid. Pairs were classified as western or glaucous-winged if (1) the only identified bird associated with a nest was a member of one of these species; or (2) both members of the pair were of one of these two species (see below). Only one mixed species pair (western × glaucous-winged) was found during this study. In the vast majority of cases both members of the pair were clearly identified (Gray's Harbor: 72%, 88 of 123; Tatoosh: 80%, 107 of 133). Therefore, we could determine if the female was paired with a male of the same phenotype (hybrid or parental species) or if the female was paired with a male of a different phenotype, as well as how this might affect breeding performance.

During regular nest checks we assessed reproductive performance in pairs of varying identity using quantified indices of breeding competence including clutch size, egg volume, hatching success, and fledging success. Our protocol for data collection on reproductive performance was as described in Pierotti (1982), Pierotti and Annett (1991), and Annett and Pierotti (1999).

Gulls typically produce a clutch of three eggs, which constrains reproductive output to a maximum of three fledged chicks per year. We monitored chick survival and condition either by direct measurement (chicks < 500 g) or through a spotting scope during nest watches (chicks > 500 g), which allowed us to assess the number of offspring fledged per nest.

Nests were checked twice weekly from late May through early August, which covered the interval from prelaying to hatching. During each nest check all pellets, food remains, and other regurgitated material were removed from the territory so they would not be recounted on subsequent visits. Separate records were maintained for food items found on each breeding territory throughout the breeding season. Because only the resident pair and their offspring were present on these territories, any food items found on a territory were assumed to be remains of food eaten by the resident pair.

Data on the composition and temporal patterning of diet for each pair was collected by use of three principal methods (Pierotti 1981, 1987a; Pierotti and Annett 1987, 1990, 1991). First, gulls regurgitate pellets consisting of undigested portions of food around their nesting territories. We collected, counted, and analyzed contents of pellets. Second, adults and chicks captured for the purpose of banding or weighing regurgitate the contents of their proventriculus. These regurgitants could be easily identified to species and often to age class and sex of fishes and marine invertebrates. The third method for identifying food items consisted of observing bouts of mate and chick feeding from a blind during nest

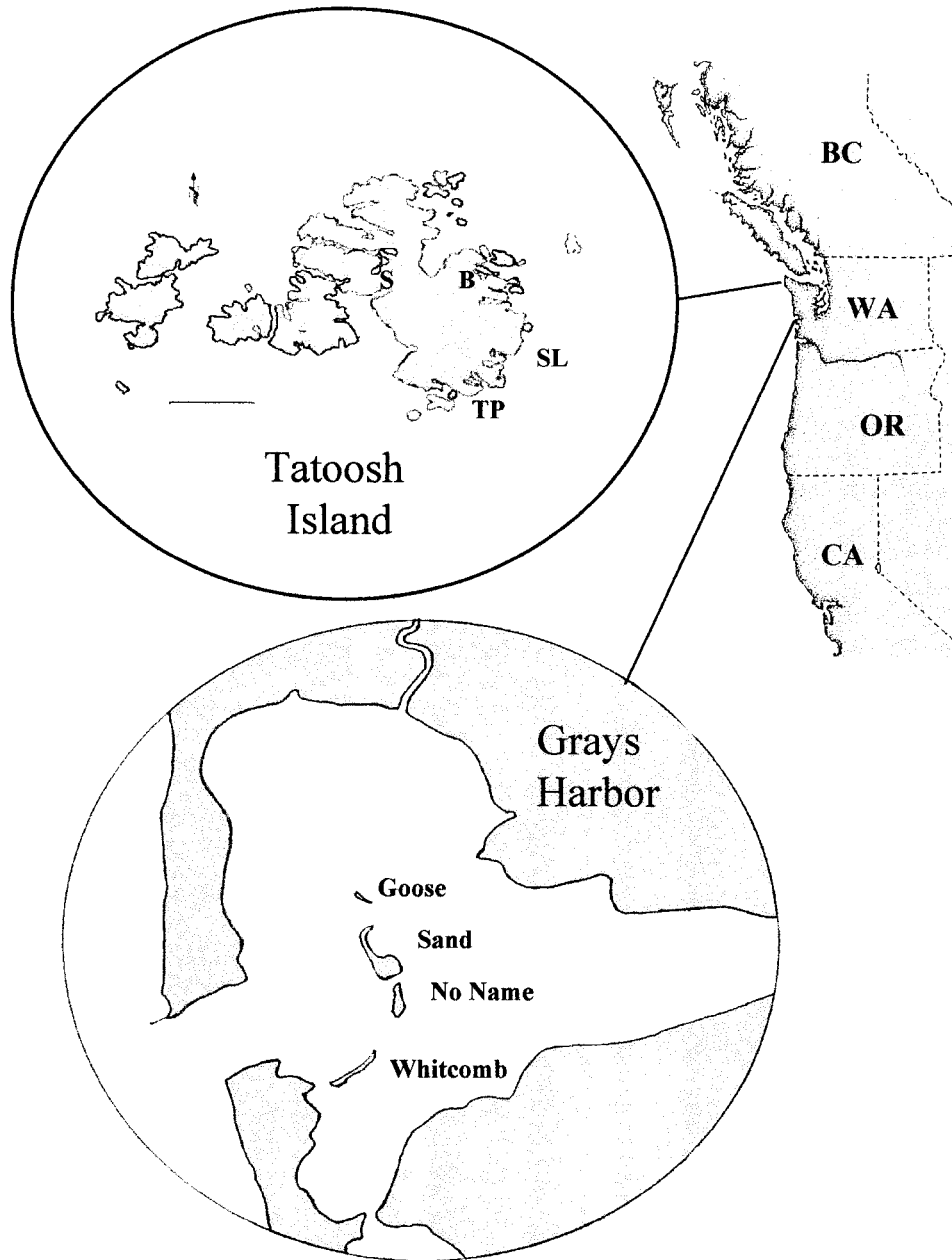


FIG. 1. Map of the area incorporated within the hybrid zone and of the two locations used in this study (Gray's Harbor and Tatoosh Island).

watches conducted for two to three hours at a time. We used telescopes and binoculars to observe transfer of food, and were able to identify type, size, and, on occasion, even number of food items. Combined data from pellets, regurgitations, and chick and mate feedings were used to generate diets for each pair.

Identification of Hybrids and Parental Species Phenotypes

Although similar in size, with extensive overlap in body measurements, glaucous-winged gulls and western gulls are readily distinguishable in the field (Hoffman et al. 1978; Verbeek 1993; Pierotti and Annett 1995). Adult glaucous-winged gulls have light gray mantles and subterminal primary feather

tips, pink legs, and a straw yellow bill. The iris is light gray, but it usually has blotches of brown pigment. The eye is surrounded by a deep pink or purple eye-ring (Hoffman et al. 1978; Bell 1992; Verbeek 1993). Adult western gulls have a dark gray mantle and nearly black primary tips, pink legs and feet, and a bill that is straw yellow (males) to orange yellow (females). The iris is straw yellow with slight brownish flecking distributed over the lower part of the iris. The eye is surrounded by a yellow to orange yellow eye-ring (Hoffman et al. 1978; Bell 1992; Pierotti and Annett 1995).

Individuals within breeding pairs were identified using a hybrid index in which traits specific to the parental taxa were quantified in the field, which is an effective method of iden-

TABLE 1. Character score (CS) given to different components of the hybrid index (from Bell 1992). The character scores were summed to provide a hybrid index. Numbers in parentheses following each character refer to the total score possible for that character. Munsell notations are from a 37-step neutral value scale. Hybrid indices ranged from 0–29 and were classified western gull (0–8), hybrid (9–19), and glaucous-winged gull (20–29).

Mantle	(7)	Primary Tips	(10)	Eye-ring	(5)	Iris pigment	(6)	Iris color	(1)
Munsell:	CS	Munsell:	CS	Color:	CS	Intensity:	CS	Color:	CS
3.25–3.50	0	1.00–1.25	0	Yellow-orange	0	Light	0	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		

tifying birds (Moore and Koenig 1986) and is highly reproducible (Hoffman et al. 1978; Bell 1992; Good 1998). Scale of the hybrid index ranged from 0 to 29, and consisted of scores for mantle color, primary tip color, eye-ring color, iris pigmentation, and iris color (Table 1). Mantle and primary pigmentation were scored by matching the plumage color to a Munsell 37-step neutral value scale. The hybrid index was constructed following Hoffman et al. (1978) and Bell (1992), such that western gulls had scores ranging from 0 to 8, hybrids had scores ranging from 9 to 19, and glaucous-winged gulls had scores ranging from 20 to 29.

Observations and characterization of traits used in the hybrid index were made during mid day when lighting conditions were optimal, using 10 × 50 Zeiss binoculars and a 20 × 60 Optolyth Zoom Spotting Scope, both of which have high-quality optics. For scoring of mantle and primary feathers, the Munsell gray scale chart was oriented toward incident light at the same angle as the gull under observation. Eye-ring and iris color were easily observed under good light conditions using our high powered optical equipment. During observations, males could easily be differentiated from females on the basis of their larger overall size, heavier heads and bills, and on the basis of roles taken during mate feeding

and copulation (Pierotti 1981, 1987a; Verbeek 1993; Pierotti and Annett 1995).

To test whether mating between gulls was nonrandom with respect to the hybrid index, intrapair Pearson product-moment correlation coefficients (r) were calculated for total hybrid index and individual traits at each location. To examine mating patterns of taxon categories derived from the hybrid index scores, we compared western gull, hybrid gull, and glaucous-winged gull pairings using contingency tables. In this paper, we do not distinguish among categories of hybrids (e.g., F_1 , backcross, etc.). Birds included in the hybrid category are all individuals with a score of 9–19 generated by our hybrid index and all were clearly intermediate between the two parental species.

RESULTS

During surveys conducted in 1995–1996 in Gray's Harbor, we found that intermediate phenotypes outnumbered western gull phenotypes by more than 2:1 and glaucous-winged gull phenotypes by more than 10:1 (Table 2). Overall numbers of intermediate phenotypes appear to have increased markedly since studies conducted in 1974–1975 (Hoffman et al. 1978) and in 1989 (Bell 1992, 1996). Bell used a hybrid index in the field and collected specimens in Gray's Harbor, and the former technique indicated fewer intergrades than did his results based on specimens collected in Gray's Harbor. Bell's ratios based on specimens yielded results intermediate between ours and those of Hoffman et al. (Bell 1992, table 31).

During surveys conducted in 1996–1997 on Tatoosh Island, intermediate phenotypes were about as common as glaucous-winged gull phenotypes and much more abundant than western gull phenotypes (Table 2). On Tatoosh there appears to have been a steady increase in the number of intermediates over the last two decades, with a concurrent decrease in the number of glaucous-winged gull phenotypes.

These results suggest that intermediates are increasing at the expense of parental phenotypes in both of our study sites, a situation also found on Destruction Island, which is located between our study sites (Table 2). It also appears that the hybrid zone may be spreading both north and south (Bell 1992; cf. Dawson 1909). All of these results support the

TABLE 2. Changes in frequency of gulls of intermediate phenotype within the hybrid zone between western and glaucous-winged gulls over the last 25 years. Data are expressed as percent of total for each study area.

	Western	Inter- mediate	Glaucous- winged
Gray's Harbor			
1. HWS 1974–75 ¹	39%	48%	13%
2. Bell 1989	50	44	6
3. This study 1995–96	25	69	6
Destruction Island			
1. HWS 1974–75 ¹	29	52	19
2. Bell 1989	23	67	10
Tatoosh Island			
1. HWS 1974–75 ¹	7	2	91
2. Bell 1989	0	35	65
3. This study 1995–96	2	48	50

¹ HWS, Hoffman et al. (1978).

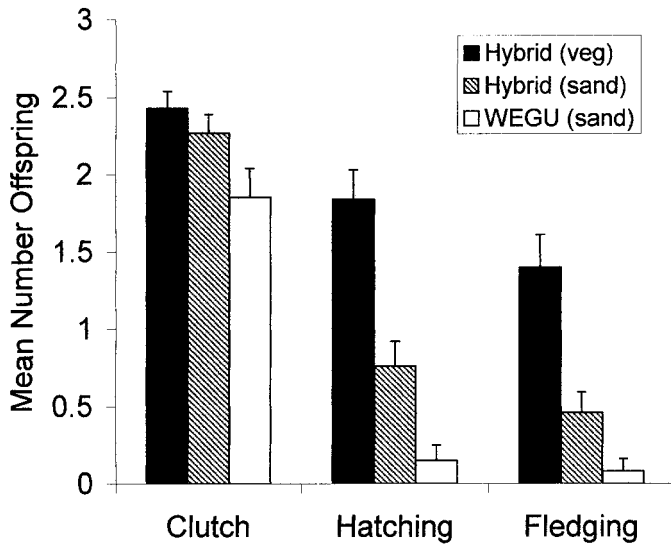


FIG. 2. Reproductive performance in relation to phenotype at Gray's Harbor. Differences in clutch size in Gray's Harbor among hybrid and western gulls are significant (Mann-Whitney $U = 27762$, $P < 0.001$). For hatching success, the difference between hybrid and western gulls is significant (Kruskal-Wallis $H = 25.4$, $P < 0.001$). For fledging success, the difference between hybrid and western gulls is also significant ($F_{2,68} = 14.6$, $P < 0.001$, Tukey's HSD $P < 0.001$). Error bars represent 1 SE.

general finding that hybrids are superior and increasing relative to both parental phenotypes in this region.

Nesting Habitat and Breeding Performance in Relation to Phenotype

One parental individual from 35 nesting pairs of gulls was identified to phenotype; in an additional 88 pairs both the male and female were identified in Gray's Harbor during 1995 and 1996. Of these 123 pairs, 90 (73%) nested in sand habitat, which consisted of exposed sand beaches and dunes, with the primary cover available being driftwood and logs. The remaining 33 pairs (27%) nested in vegetated habitat, which consisted primarily of tall grass (0.5–1.0 m high) or reeds (2–4 m high) that provided dense cover for nests, chicks, and

nesting adults. On Tatoosh Island during 1996 and 1997, phenotype of one member was identified from 26 nesting pairs, and from an additional 107 pairs both the male and female were identified. Of these 133 pairs, 89 (67%) nested in rock habitat (bare exposed marine terrace) and 44 (33%) nested in vegetated habitat (0.5–1.0 m high).

In Gray's Harbor there was a strong association between parental phenotype and habitat type. During 1996, almost all (93%) pairs nesting in vegetated habitat were identified as hybrid, whereas in open (sand) habitat, 77% were identified as hybrids and 23% were identified as western gull ($\chi^2 = 4.5$, $df = 1$, $P = 0.03$). Clutch sizes of pairs identified as western gull in sand habitat (1.85 ± 0.19 , $n = 13$) were significantly smaller than those of pairs identified as hybrid in both sand (2.27 ± 0.12 , $n = 44$) and vegetated habitat (2.43 ± 0.11 , $n = 28$; Fig. 2). Gulls in vegetated habitat laid primarily two- and three-egg clutches (96%), whereas only 15% of pairs identified as western gull in sand habitat produced three-egg clutches.

Although differences in clutch size indicate that gulls nesting in vegetated habitat have higher overall breeding success, gulls nesting in sand habitat produced significantly larger A, B, and C eggs (Table 3). In fact, many eggs laid in sand habitat weighed well over 100 g, which makes them much heavier than eggs laid by western gulls on other colonies (Pierotti and Annett 1995). Egg size is often used as an indicator of phenotypic quality (Pierotti 1982; Bell 1992). As a result, the superior breeding performance in vegetated habitat may have been more the result of habitat choice than of phenotypic superiority.

On Tatoosh Island, both hybrids and glaucous-winged gulls nested randomly in both rocky and vegetated habitat ($\chi^2 = 0.009$, $df = 1$, $P = 0.92$). There were no significant differences in clutch size among nests of identified hybrids in vegetated habitat (2.50 ± 0.14 , $n = 28$) or in rock habitat (2.56 ± 0.09 , $n = 59$) and glaucous-winged gull nests in rock (2.55 ± 0.14 , $n = 20$) and vegetated habitat (2.57 ± 0.30 , $n = 7$; Fig. 3). In contrast to Gray's Harbor, there were no significant differences in egg size among habitats (Table 4).

Hybrids nesting in both vegetated and sand habitats in

TABLE 3. Dimensions of 1st-laid (A), 2nd-laid (B) and 3rd-laid (C) eggs (length and breadth in mm; volume and volume difference in cm^3) of pairs in Gray's harbor. Sample size for each habitat type (sand/vegetated) in brackets. Data presented as mean \pm SD. Mann-Whitney U -values shown in braces for tests where data were not normally distributed.

Dimensions	Sand	Vegetated	t	df	p
Length					
A egg [354/317]	72.5 \pm 2.838	71.5 \pm 2.809	4.7	668	< 0.001
B egg [179/237]	72.0 \pm 2.852	70.8 \pm 2.850	4.0	415	< 0.001
C egg [84/113]	71.4 \pm 2.705	70.6 \pm 2.341	2.3	194	0.021
Breadth					
A egg [354/317]	49.7 \pm 1.392	49.2 \pm 1.592	{66263}		< 0.001
B egg [179/237]	49.6 \pm 1.342	49.2 \pm 1.624	{24697}		0.005
C egg [84/113]	49.1 \pm 1.479	48.6 \pm 1.391	2.5	194	0.014
Volume					
A egg [354/317]	85.4 \pm 6.607	82.6 \pm 6.678	5.5	668	< 0.001
B egg [179/237]	84.4 \pm 6.149	81.9 \pm 6.95	3.8	415	< 0.001
C egg [84/113]	82.2 \pm 6.082	79.6 \pm 5.90	3.0	194	0.003

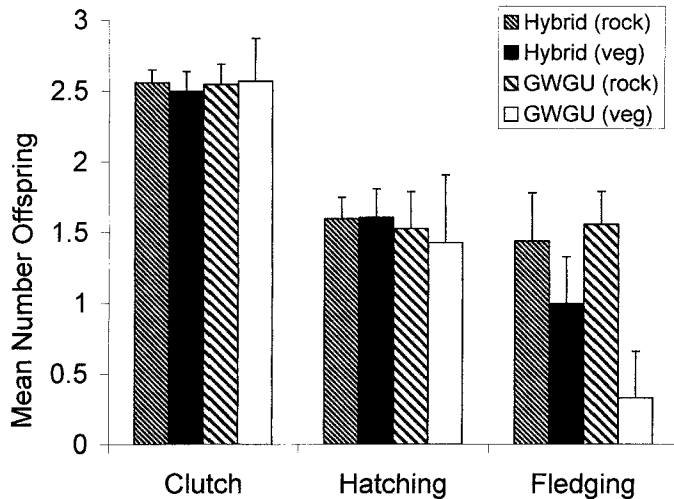


FIG. 3. Reproductive performance in relation to phenotype on Tatoosh Island. Differences in clutch size, hatching success, and fledging success both among habitats and between hybrids and glaucous-winged gulls are not significant ($F_{3,110} = 0.05$, $P = 0.98$; $F_{3,34} = 1.85$, $P = 0.16$). Error bars represent 1 SE.

Gray's Harbor in 1996 had greater mean hatching success (sand = 1.84 ± 0.19 chicks/nest, $n = 25$; vegetated = 0.76 ± 0.16 chicks/nest, $n = 41$) than did western gulls in sand habitat (0.15 ± 0.10 chicks/nest, $n = 13$; Fig. 2). These differences in hatching success appeared to be related to disturbance and predation caused by bald eagles, *Haliaeetus leucocephalus*, which are present in substantial numbers in Gray's Harbor. We regularly observed five to 10 panic flights per day among gulls nesting in sand habitat resulting from eagle flyovers, and we observed as many as 16 eagles on our study colonies at one time (Good 1998). Eagles were also observed to take adults, chicks, and eggs of gulls as prey. In addition, a high level of egg predation by gulls occurred during disturbances caused by eagles. Gulls nesting in vegetated habitat were much less disturbed by eagles, and their eggs were sheltered even if the parent birds flew away from the nest. As a result, nests in vegetated habitat were much less vulnerable to egg predation.

Patterns of chick fledging paralleled those of chick hatching. In Gray's Harbor, hybrids nesting in vegetated and sand habitats had greater fledging success (sand = 1.40 ± 0.21 fledglings/pair, $n = 25$; vegetated = 0.46 ± 0.13 fledglings/pair, $n = 41$) than did western gulls nesting in sand habitat (0.08 ± 0.08 fledglings/pair, $n = 35$; Fig. 2). This difference also appeared to be the result of eagle predation and disturbance, because vegetated habitat provided many more hiding places for chicks than did the open sand habitat, and chicks in sand habitat often disappeared, which suggests that they were taken as prey by eagles.

On Tatoosh Island, hybrids in both rock and vegetated habitat hatched more chicks per nest (rock = 1.60 ± 0.15 chicks/nest, $n = 52$; vegetated = 1.61 ± 0.20 chicks/nest, $n = 28$) than did glaucous-winged gulls (rock = 1.53 ± 0.26 chicks/nest, $n = 17$; vegetated = 1.43 ± 0.48 chicks/nest, $n = 7$; Fig. 3); however, these differences among types were not statistically significant. This pattern continued into the fledging period, with hybrids in both habitats pooled having

TABLE 4. Dimensions of 1st-laid (A), 2nd-laid (B), and 3rd-laid (C) eggs (length and breadth in mm; volume and volume difference in cm^3) of pairs on Tatoosh Island. Sample sizes for each habitat type (sand/vegetated) in brackets. Data presented as mean \pm SD. Mann-Whitney U -values shown in braces for tests where data were not normally distributed.

	Rock	Vegetated	t	df	p
Length					
A egg [90/68]	72.0 ± 3.01	72.2 ± 2.93	0.5	156	0.6
B egg [83/63]	71.0 ± 2.82	71.2 ± 2.47	0.9	144	0.4
C egg [60/48]	70.6 ± 2.63	71.1 ± 2.52	0.9	106	0.3
Breadth					
A egg [90/68]	49.8 ± 1.49	49.3 ± 1.97	{3484}		0.1
B egg [83/63]	49.8 ± 1.43	49.6 ± 1.68	0.8	144	0.4
C egg [60/48]	49.0 ± 1.44	48.8 ± 1.20	0.7	106	0.5
Volume					
A egg [90/68]	85.3 ± 6.65	83.8 ± 8.22	1.2	156	0.2
B egg [82/63]	83.9 ± 6.54	83.7 ± 7.23	0.2	144	0.9
C egg [60/48]	80.8 ± 5.99	80.8 ± 5.98	0.01	106	0.9

higher fledging success (1.38 ± 0.27 fledglings/pair), compared to glaucous-winged gulls (1.17 ± 0.33 fledglings/pair; Fig. 3), however, this difference was also not significant. Although bald eagles are present on Tatoosh, the level of disturbance was much lower, and predation was directed primarily at common murre, *Uria aalge* (Parrish 1995).

In addition to choice of nesting habitat, diet may also play a role in determining relative reproductive performance within the hybrid zone. In Gray's Harbor, diet differed more between subcolonies than between phenotypes (Ellis 1997). On Tatoosh Island, diets differed between phenotypes. Hybrids took a diet composed predominantly of fish (52.2%) with pelagic barnacles (47.8%) making up the balance, whereas diets of glaucous-winged gulls on Tatoosh consisted primarily of intertidal invertebrates (67.8%) with some fish (28.6%; Ellis 1997).

Mate Choice, Pair Category, and Reproductive Success

There was only weak evidence of assortative mating in Gray's Harbor and no evidence of assortative mating on Tatoosh. Correlations between male and female hybrid indices were not large (Gray's Harbor: $r^2 = 0.16$, $0.05 < P < 0.01$; Tatoosh: $r^2 = 0.04$, $P > 0.10$). In Gray's Harbor, the weak assortative mating resulted primarily from the absence of mixed species pairs and the tendency of intergrades to pair with other intergrades. Of the females identified, most western gull females were paired with hybrid males and most hybrid females also paired with hybrid males ($\chi^2 = 19.6$, $df = 4$, $P = 0.002$). On Tatoosh, pairing appeared to be nearly random, with as many female glaucous-winged gulls paired to male hybrids as to conspecific males ($\chi^2 = 5.0$, $df = 4$, $P = 0.40$).

We obtained complete data on reproductive performance for 73 pairs in Gray's Harbor during 1995 and 1996 and 74 pairs nesting on Tatoosh Island during 1996 and 1997 in which both individuals within the pair were identified to phenotype. In Gray's Harbor in 1996, regardless of their own phenotype, females paired with hybrid males produced larger clutches than those paired to western gull males (Mann-Whit-

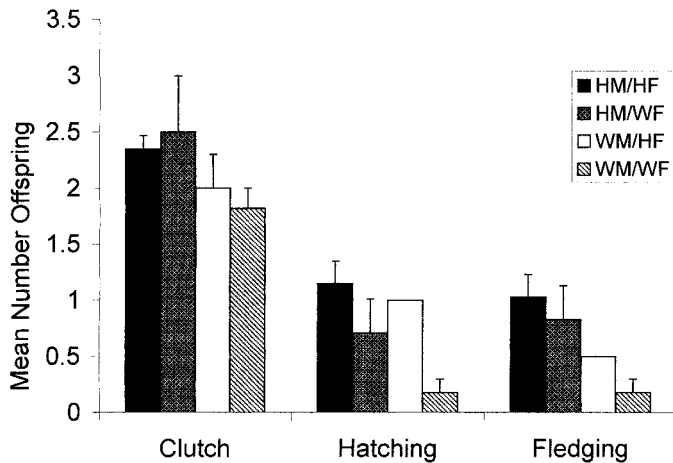


FIG. 4. Reproductive performance in pairs in which both members of the pair were identified for four pair categories in each study area at Gray's Harbor: (1) pure hybrid; (2) hybrid male/parental female; (3) parental male/hybrid female; and (4) pure parental pair. Differences in clutch size are significant between pairs with hybrid male and pairs with a western gull male by ANOVA ($F_{2,82} = 2.87$, $P = 0.06$). Differences in hatching success are significant between pair categories (Kruskal-Wallis $H = 22.2$, $0.05 < P < 0.01$). Differences in fledging success are also significant between pair categories (Kruskal-Wallis $H = 20.9$, $0.05 < P < 0.01$). Error bars represent 1 SE.

ney test, $U = 27762$, $P < 0.001$). (1) male hybrid/female western gull pairs (2.50 ± 0.50 , $n = 16$) and (2) pure hybrid pairs (2.35 ± 0.12 , $n = 46$) compared to (3) male western gull/female hybrid pairs (2.00 ± 0.30 , $n = 5$) and (4) pure western gull pairs (1.82 ± 0.18 , $n = 13$) (Fig. 4).

Pure hybrid pairs also hatched the most chicks (1.15 chicks/nest, $n = 33$), followed by western gull females paired to hybrid males (0.71 chicks/nest, $n = 16$), and pure western gull pairs (0.15 chicks/nest, $n = 13$; Fig. 4). Pure hybrid pairs also had the highest fledging success (1.03 fledglings/pair, $n = 32$), followed again by western gull females paired to male hybrids (0.73 fledglings/pair, $n = 15$), and pure western gull pairs (0.15 fledglings/pair, $n = 13$; Fig. 4). These differences were the result of heavy predation on eggs in sand habitat, where male western gulls established breeding territories. We only observed two of several hundred pure western gull chicks to hatch and fledge during this study, with all other offspring being depredated either as eggs or chicks. In contrast, females paired to hybrid males were less vulnerable to egg and chick predation because many hybrid males established breeding territories in vegetated habitat, where predation was greatly reduced.

On Tatoosh Island, clutch size did not differ significantly between pairs with hybrid males compared to pairs with glaucous-winged males: (1) pure hybrid pairs (2.49 ± 0.11 , $n = 35$) and (2) female glaucous-winged gull/male hybrid pairs (2.61 ± 0.16 , $n = 18$) compared to (3) female hybrid/male glaucous-winged gull pairs (2.55 ± 0.17 , $n = 20$) and (4) pure glaucous-winged gull pairs (2.56 ± 0.12 , $n = 27$) (Fig. 5). There were differences in hatching success, however, with females paired to hybrid males showing better success (glaucous-winged gull female/hybrid male pairs: 2.2 chicks/nest, $n = 15$; pure hybrid pairs: 1.77 chicks/nest, $n = 33$; female

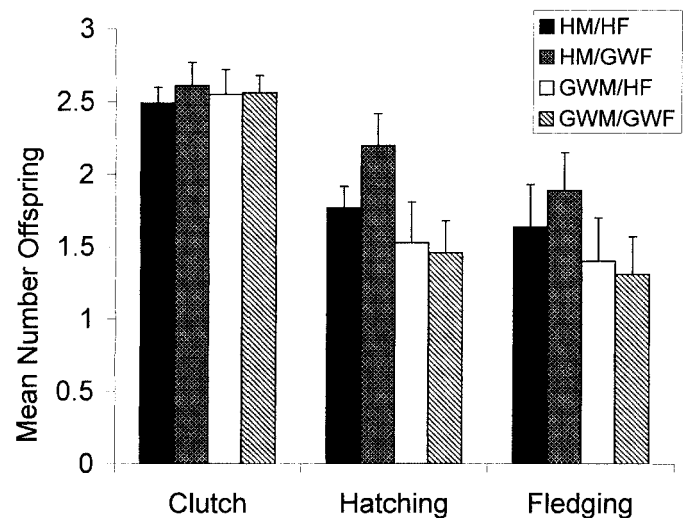


FIG. 5. Reproductive performance in pairs in which both members of the pair were identified for four pair categories on Tatoosh Island: (1) pure hybrid; (2) hybrid male/parental female; (3) parental male/hybrid female; and (4) pure parental pair. Differences in clutch size among pair categories are not significant. Differences in hatching success (Kruskal-Wallis $H = 18.2$, $0.01 < P < 0.05$) and fledging success (Kruskal-Wallis $H = 16.3$, $0.05 < P < 0.1$) are significant between pairs with hybrid males and pairs with glaucous-winged gull males. Error bars represent 1 SE.

hybrid/glaucous-winged gull male pairs: 1.53 chicks/nest, $n = 19$; pure glaucous-winged gull pairs: 1.46 chicks/nest, $n = 24$; Fig. 5). For fledging success on Tatoosh, females paired to hybrid males also did better (female glaucous-winged gull/hybrid male pairs: 1.67 fledglings/nest, $n = 9$; pure hybrid pairs: 1.64 fledglings/nest, $n = 14$; female hybrid/male glaucous-winged gull pairs: 1.40 fledglings/nest, $n = 10$; pure glaucous-winged gull pairs: 1.31 fledglings/nest, $n = 13$; Fig. 5).

DISCUSSION

Our results demonstrate that pure hybrid or mixed pairs did as well or better in terms of reproductive success than did pure parental pairs at both sections of the hybrid zone. This difference appears to result primarily from females pairing with hybrid males. We argue that higher reproductive success is associated with the tendency of gulls of intermediate phenotype to have behavior that combines adaptive traits of both parental species in this ecological setting, where choice of breeding habitat appears to be the primary determinant of reproductive success in Gray's Harbor and choice of diet may be the strongest influence on Tatoosh.

The primary range of western gulls is along the coast of California, extending into Oregon, and almost all nesting colonies are located on offshore islands that are rocky or have low vegetation (Hoffman et al. 1978; Pierotti 1981; Pierotti and Annett 1995). During the gull breeding season, rainfall is light to nonexistent in these areas (Pierotti 1981; Ainley and Boekelheide 1990). In addition, these nesting islands are typically free of predators, with the exception of conspecifics. As a consequence, there has been little or no selective pressure for western gulls to nest under shelter, and

during its evolution this species has nested almost exclusively in open habitat, avoiding tall vegetation throughout its range (Hoffman et al. 1978; Pierotti and Annett 1995).

In contrast, glaucous-winged gulls primarily inhabit coastal estuaries from central Oregon up through Alaska and throughout the Aleutian Islands (Verbeek 1993). Many nesting islands on which glaucous-winged gulls live contain extensive tall vegetation, as a result of abundant rainfall during the breeding season. These islands often contain predators, including bald eagles, northwestern crows (*Corvus brachyrhynchos*), and ravens (*Corvus corax*), which certainly take eggs and chicks (Verbeek 1993). As a consequence of both rainfall and predation, glaucous-winged gulls require more sheltered nesting sites and often nest deep in heavy vegetation (Hoffman et al. 1978; Verbeek 1993). In fact, earlier studies within the hybrid zone indicated that the presence or absence of glaucous-winged gulls on a colony was determined by the presence of tall grass (Hoffman et al. 1978). These differences in nesting ecology between the parental species suggest that hybrid males showed significantly better breeding performance in Gray's Harbor because hybrid males are more like glaucous-winged gulls in their choice of nesting habitat, thus establishing nesting territories that provide greater protection from predation.

Hybrids also showed slightly better hatching and fledging success on Tatoosh Island, where there was little difference in nesting habitat choice, but there were differences in diet. The western gull is an outer coastal maritime species that takes primarily pelagic prey, especially fish, but also euphausiids and squid (Pierotti 1981; Ainley and Boekelheide 1990; Pierotti and Annett 1995; Ellis 1997). Within western gulls there is considerable individual variation in diet, with those individuals that take a higher percentage of fish showing enhanced egg and clutch size, hatching success, and chick growth and survival (Pierotti and Annett 1987, 1990; Annett and Pierotti 1989, 1999). The glaucous-winged gull is a species of coastal maritime habitat and intercoastal waterways, whose diet also varies from colony to colony, but appears to be dominated by intertidal organisms, with fish and the eggs and young of other species of seabird making up most of the remainder (Trapp 1979; Murphy et al. 1984; Irons et al. 1986; Verbeek 1993; Ellis 1997).

On Tatoosh Island, the differences in breeding success among phenotypes may be attributable to significant differences in diet between phenotypes. Diets of glaucous-winged gulls on Tatoosh consisted primarily of intertidal invertebrates, which is typical for the species (Ellis 1997). In contrast, hybrids took predominantly fish, followed by pelagic barnacles (Ellis 1997). The primary effects of a fish diet appear to be on hatching success and chick growth (Annett and Pierotti 1989, 1999; Pierotti and Annett 1990). The only significant differences among phenotypes on Tatoosh were in hatching and fledging success, which suggests that hybrids, which took a fish diet more typical of western than of glaucous-winged gulls, may have produced more viable eggs and healthier chicks despite overall similarity in clutch and egg sizes. In addition, the larger eggs produced by gulls nesting in sand habitat in Gray's Harbor may also have resulted from dietary differences, because western gulls and western gull-like intergrades were most abundant in this habitat, and diet

quality is known to influence egg size in gulls (Pierotti and Bellrose 1986; Pierotti and Annett 1987, 1990, 1991).

As a result of differences resulting from habitat choice in Gray's Harbor and diet choice on Tatoosh, female gulls who chose hybrid males as mates did better overall than did females mated to conspecific males. This provides support for the idea of bounded hybrid superiority because there is no short-term selection against females that choose males outside of their taxon. In fact, there appears to be rather strong selection favoring females who chose hybrid males in Gray's Harbor. It is possible that the difference in reproductive performance in Gray's Harbor yields high frequencies of intermediate phenotypes in this area and may even be driving the entire hybrid zone. Our results indicate an increase in intermediate phenotypes of 25% since 1989, a change in proportion that seems to have resulted from an overall increase in hybrid phenotypes, combined with a reduction in number of western gull phenotypes due to the heavy predation on eggs, chicks, and even adults of the latter.

Early studies of reproductive performance within the hybrid zone (Hoffman et al. 1978) suggested that the hybrid zone was in equilibrium because of the counterbalancing effects of higher reproductive success by intergrades and immigration by parental forms from outside the hybrid zone. Subsequent research (Bell 1992, 1996) indicated that the hybrid zone is expanding, primarily at the expense of glaucous-winged gulls: Intermediate phenotypes increased on Tatoosh from 2% in 1974–1975 (Hoffman et al. 1978) to 35% in the late 1980s. Our data indicate additional increases in the frequency of intergrades in the northern part of the hybrid zone (Table 2). These results suggest two potential interpretations: (1) in contrast to the simulation model of Hoffman et al. (1978), immigration by intergrades into more northern colonies may be swamping any southward immigration by glaucous-winged gulls; or (2) western gulls and hybrids may be superior competitors over glaucous-winged gulls. In a study of sympatric gull species in the Netherlands, where hybridization was not found to occur, the pelagic foraging lesser black-backed gull (*Larus fuscus*) was more successful at reproduction, and was displacing the larger, intertidal foraging herring gull (*L. argentatus*; Noordhuis and Spaans 1992). Our results on Tatoosh Island suggest a similar scenario, where pelagic foraging hybrids appear to be increasing relative to glaucous-winged gulls.

Other avian hybrid zones have shown variation in both mating patterns and reproductive success. Positive assortative mating by overall plumage phenotype was found in the carrion crow (*Corvus corone corone*)/hooded crow (*C. c. cornix*) hybrid zone in Italy, but not in Scotland (Saino and Bolzern 1992; Saino and Villa 1992). In *Geospiza* finches on Daphne Major, (*G. fortis* × *G. scandens*) F₁ hybrids showed positive mating assortment, whereas (*G. fortis* × *G. fuliginosa*) F₁ hybrids showed negative mating assortment with respect to size, and first generation backcrosses mated randomly with respect to both size and paternal song (Grant and Grant 1997b). Similarly, yellow-shafted (*Colaptes auratus auratus*) and red-shafted flickers (*C. a. cafer*) appear to mate randomly. Specimens from this hybrid zone have been compared from 1890 through 1981, with no detectable evolution of premating reproductive isolation (Moore and Buchanan 1985). Within

this flicker hybrid zone, clutch size in heterospecific pairs was equivalent to that of conspecific pairs and hatchling survivorship did not differ among six phenotype pairings (Moore and Koenig 1986). Additionally, hatchling survivorship for yellow-shafted females was equivalent regardless of whether they were paired with yellow-shafted or hybrid males, and for red-shafted females, hatchling survival was greater when paired with a hybrid male (Moore and Koenig 1986).

These results may be relevant to our understanding of both the process of speciation and the nature of species. Naturally occurring hybridization presents problems for some widely used species concepts, including the biological or isolation species concept (Mayr 1963) and the recognition species concept (Paterson 1985), because the occurrence of widespread hybridization indicates that reinforcement (either reproductive isolation or species recognition mechanisms) may not be functioning in a manner adequate to preserve species integrity. In most hybrid zones involving animal species, there is presumed to be evidence of assortative mating, selection against hybrids, and reinforcement of prezygotic isolating mechanisms by postzygotic isolating mechanisms (Barton and Hewitt 1985; Hewitt 1988). None of these phenomena were observed in our study areas, however, or in several other avian hybrid zones mentioned.

Avian hybrid zones may prove to be more the exception than the rule with regard to reinforcement. In birds, it has been argued that behavioral barriers to interbreeding evolve first, with postmating isolation usually evolving later, thus increasing the opportunity for introgressive hybridization and reducing the scope for reinforcement of premating isolation (Grant and Grant 1997a).

Avian hybrid zones are probably best regarded as regions of steep genotypic transition between populations that have reached a level of divergence such that the parental populations retain their taxonomic identity and integrity, even though reproductive isolation may be incomplete or even wholly lacking (Moore and Price 1993). In such cases, there should be uniformity of genotype within the parental "species" and discontinuity between the genotypes of different species. Under such conditions, even if hybrids are not well adapted to the environment of either parental form, they may be better adapted in the hybrid zone, yielding "geographically bounded hybrid superiority" (Moore 1977). Our study provides one of the best supported examples of such hybrid superiority, and because hybrids or intergrades appear to have been superior to parental types for at least 25 years, reproductive isolation or specific mate recognition mechanisms appear to be largely irrelevant within this hybrid zone.

Despite this extensive hybridization and the apparent superiority of hybrids, we agree with earlier investigators who have contended that western and glaucous-winged gulls should continue to be recognized as separate species (Hoffman et al. 1978; Bell 1996). Outside the hybrid zone, selection should enforce the uniformity of genotype within each "parental" species, but the sustained cohesion of the hybridizing taxa in combination with the discontinuity of genotype observed within the hybrid zone implies that forces more fundamental than simple reinforcement are involved in speciation (Moore and Price 1993).

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