Influence Of Nesting Habitat In The Western/Glaucous-Winged Gull Hybrid Zone: A Preliminary Study by Thomas P. Good, Raymond J. Pierotti and Julie C. Ellis

The large, white-headed gulls of the genus Larus have a northern circumpolar distribution, and often hybridize in areas where they come into contact. Over 50% of 42 recognized species of Larus are known to hybridize (Pierotti 1987a), and at least two taxa are thought to be of hybrid origin (Panov 1989). The Glaucous-winged Gull Larus glaucescens breeds in North America from the Aleutian Islands in Alaska southward along coastal British Columbia and Washington to Oregon (Bell 1992). In regions of breeding sympatry, L. glaucescens interbreeds with Glaucous Gulls Larus hyperboreus in the Bering Sea (Strang 1977) and Herring Gulls Larus argentatus in southeastern Alaska (Patten 1980). The largest region of overlap and hybridization is with the Western Gull Larus occidentalis from northern Puget Sound in Washington to the central Oregon coast (Bell 1996).

Hoffman et al. (1978) identified pairs on Destruction Island, Washington as "pure" or "hybrid" and reported apparent assortative mating. Hybrid pairs at that colony showed higher hatching success than did pairs of L. occidentalis or L. glaucescens. Subsequent work at several sites found egg volume and clutch size of hybrids intermediate between L. occidentalis and L. glaucescens, suggesting a complex, dynamic situation (Bell 1992).

The ecological and behavioral processes maintaining this hybrid zone have yet to be understood. The breeding ecology of pairs with one or more hybrids may be like that of either parental taxon, or it may be unique to hybrids. Breeding success in gulls can be influenced by nesting habitat selection and territory quality (Pierotti 1982, Pierotti 1987b) and parental attendance (Pierotti 1981, 1987b, Morris 1987). As part of a larger study to test competing hypotheses of hybrid zone maintenance, we tested hypotheses that 1) nest-site characteristics vary among habitats and 2) breeding success varies among habitats for breeding pairs at colonies within the hybrid zone.

Methods
The study was conducted on four islands in Gray's Harbor, along the southern coast of Washington, at the approximate mid-point of the L. glaucescens/L. occidentalis hybrid zone. Sand Island (46°57'45"N, 124°03'25"W), Goose Island (46°58'40"N, 124°04'10"W) and an unnamed island (46°57'30"N, 124°03'05"W) are islands located in the northern bay, and Whitcomb Flats (46°54'40"N, 124°04'40"W) is an island located in the southern bay. Sand Island, Goose Island and Whitcomb Flats, in addition to the focal species, have had breeding populations of Ring-billed Gulls Larus delawarensis, Double-crested Cormorants Phalacrocorax auritus and Caspian Terns Sterna caspia (Speich and Wahl 1989). The islands range from sandbars with drift logs and sparse vegetation (American Seabeach rocket Cakile edentula and Seabeach Sandwort Honkenya peploides) to islands with large, dense patches of dunegrass Elymus mollis and beachgrass Ammophila arenaria punctuated by Pacific Willow Salix lucida and stands of the reed Phragmites australis. Herbaceous species grow interspersed with the grasses, reflecting seaside plant communities of the nearby mainland.

During egg-laying in May 1995, we marked and numbered 432 nests on the four colonies by attaching flagging to vegetation or driftwood stuck in the sand or writing directly on drift logs adjacent to nests. For each nest, we categorized 1) nesting habitat as sand, grass or reed, 2) its colony position as center or edge, and 3) the natural screen adjacent to the nest (wood, grass, reed). We measured the angular extent (°) of natural screens adjacent to nests, including clutch size, hatching rate, chick survival to two weeks, fledging rate were arcsec-transformed to achieve homogeneous variances prior to analyses of variance.

Results
Of 325 active nests (those with at least one egg) on the four colonies, 179 were in "sand", 110 were in "grass" (primarily dunegrass, beachgrass, sedges Carex spp. and the herb Potentilla anserina) and 36 nests were in reed habitat (Phragmites australis). Nest microhabitat measurements varied among the three habitats. The mean angular extent (°) of natural screens adjacent to nests was greater in reeds (275 ± 12) and grass (236 ± 9) than in sand (26 ± 4) (F2, 322 = 99.5, p<0.001; Tukey HSD p<0.05). The percent of natural screens which blocked the nearest neighbor was greater in reeds (88%) and grass (80%) than in sand (13%) (2 = 223, df = 2, p<0.001). Nestling density varied among habitats; nearest neighbor distances (°) were significantly lower in reeds (3.9 ± 0.2m) and grass (3.9 ± 0.3m) than in sand (6.2 ± 0.4) (F2, 322 = 5.5, p=0.005; Tukey HSD p<0.05).

Breeding success at these colonies was extremely low overall and was strongly influenced by nesting habitat. The proportion of large clutch sizes was greatest in reeds; one-egg clutches were most common at nests in sand habitat and two and three egg clutches were more common at nests in grass and reed habitats (2 = 60.5, df = 4, p<0.01; Figure 1). Hatching rate was greatest in reed habitat and lowest in sand habitat (2, 322 = 19.6, p<0.001). Chick survival rate to two weeks was greater in reed and grass habitats than in sand habitat (2, 322 = 16.6, p<0.001). Fledging rate was greater in reed and grass habitats than in sand habitat (2, 311 = 24.4, p<0.001) (Figure 2).
Great Black-backed Gull

Nests in reed and grass habitat are closely spaced and surrounded by structure which is more likely to separate nearest neighbors. This can reduce aggression among territories in sand habitat in terms of screening adjacent to the larger and more aggressive neighbors (Cezilly and Quenette 1988) and enable pairs to nest more densely (Davis and Dunn 1976, Vermeer et al. 1988, Bukacinska and Bukacinski 1993, but see Murphy et al. 1984). Natural screens other than vegetation can act as visual or physical barriers; the heterogeneity of rocky habitats enables Herring Gulls to nest more densely (Pierotti 1982, 1987b), often directly related to extent or distribution of vegetation (Burger 1974, Jehl and Chase 1987). Rates of egg loss were extremely high at nests in sand habitat, where neighbor interactions and aggression were highest and nest attendance lowest. In the reeds, pairs that nested down tunnels lost few eggs. Pairs spent almost no time interacting with neighbors and a great deal of time loafing nearby in adjacent clearings. Pairs in reed habitat also initiated breeding earlier than in grass or sand habitats, which may contribute to greater nest success.

Predation by congeners was the primary cause of egg loss. While few gulls were egg specialists, occasional predation was widespread. Bald Eagles Haliaeetus leucocephalus are opportunistic predators on gull eggs, chicks and adults. We found evidence of eagle predation more often in sand and grass habitats than in reed habitat. Eagles affected breeding success indirectly; adult gulls fly up off nests en masse in response to eagles ("dreads"), creating opportunities for egg predation by gulls. Eagle abundance on the islands varied considerably.

We regularly recorded up to 10 eagle observations/day, and we observed dreads several times daily. On May 23, we simultaneously observed 2 adults and 5 juveniles on Sand Island and 2 adults and 7 juveniles on "No Name" Island. Egg loss due to eagle presence devastates breeding murres Uria aalge on Tatoosh Island, Washington (Parrish 1995) and cormorants Phalacrocorax auritis and P. pelagicus on Mandarte Island, British Columbia (Verbeek 1982) by creating predation opportunities for gulls and Northwestern Crows Corvus caurinus. Gull breeding success due to egg loss in Gray's Harbor (0.03 chicks fledged/egg) was lower than the lowest breeding success reported for L. glaucus (0.10; Murphy et al. 1984) or L. occidentalis at the Farallon Islands, California (0.25 in the El Nino year of 1983; Penniman et al. 1990). On these islands, selecting habitats that minimize egg predation undoubtedly increases annual and lifetime breeding success.

This hybrid zone appears to be stable (Bell 1992). Future research will determine if this is due to hybrid inferiority balanced by gene flow (dynamic equilibrium), or if hybrids which may be mal-adapted in the parental communities may be relatively well-adapted in the area of mixed ecology (geographically bounded superiority) (Moore 1977). We will test the above hypotheses by comparing patterns of habitat choice, diet, mate and chick feeding regimes, incubation and brooding attention and territory and chick guarding among breeding pairs (L. occidentalis, L. glaucus, hybrids and combinations thereof). Gray's Harbor may be unique; half of the breeding individuals are hybrids (phenotypically intermediate). Additional study sites in the hybrid zone (Destruction, Tatoosh and Protection Islands, WA) will be investigated to test the importance of habitat selection and proportion of hybrid phe-

Discussion

Nest-site characteristics and measures of breeding success varied significantly among nesting habitats at these colonies. Nests in reed and grass habitat are closely spaced and surrounded by structure which is more likely to separate nearest neighbors. This can reduce aggression among neighbors (Cezilly and Quenette 1988) and enable pairs to nest more densely (Davis and Dunn 1976, Vermeer et al. 1988, Bukacinska and Bukacinski 1993, but see Murphy et al. 1984). Natural screens other than vegetation can act as visual or physical barriers; the heterogeneity of rocky habitats enables Herring Gulls to nest more densely (Pierotti 1982, 1987b), especially when avoiding nesting adjacent to the larger and more aggressive Great Black-backed Gull Larus marinus (Good ms). Group defense is enhanced by breeding colonially, however predation on eggs and chicks, especially by conspecifics, may be facilitated by dense nesting (Hunt and Hunt 1976, Pierotti 1982, 1987b), often directly related to extent or distribution of vegetation (Burger 1974, Jehl and Chase 1987). Rates of egg loss were extremely high at nests in sand habitat, where neighbor interactions and aggression were highest and nest attendance lowest. In the reeds, pairs that nested down tunnels lost few eggs. Pairs spent almost no time interacting with neighbors and a great deal of time loafing nearby in adjacent clearings. Pairs in reed habitat also initiated breeding earlier than in grass or sand habitats, which may contribute to greater nest success.

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Figure 1. The distribution of clutch sizes in sand, grass and reed habitats on islands in Grays Harbor, Washington.
References


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Figure 2. Breeding success of gulls as a percent of eggs laid in sand, grass and reed habitats on islands in Grays Harbor, Washington. "Viable" includes all but addled eggs. Error bars represent 1SE. (*=p,0.05 by Turkey HSD test)