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BREEDING SUCCESS IN THE WESTERN GULL × GLAUCOUS-WINGED GULL COMPLEX: THE INFLUENCE OF HABITAT AND NEST-SITE CHARACTERISTICS

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Abstract. The nesting ecology of breeding pairs of the Western Gull × Glaucous-winged Gull (*Larus occidentalis* × *glaucescens*) hybrid complex was investigated at two locations in coastal Washington. In Grays Harbor, breeding performance (clutch size, hatching and fledging success) was highest in vegetated habitat where nests were most dense and where natural screens blocked the nearest neighbor. Egg loss, presumably from gull predators, was common except in areas of dense vegetation. At Tatoosh Island, egg loss was rare, and breeding performance was similar in vegetated and rock habitats. To test if physical structure around open-area nests influenced egg loss in Grays Harbor, predator-exclusion fences were erected around nests on a sandbar island lacking vegetation. Excluding predators reduced egg loss and increased hatching success relative to nests with adjacent natural screens (driftwood logs >30 cm tall) or nests lacking natural screens. Pairs that nest in habitats with adequate habitat structure appear to benefit in terms of lower egg loss and higher nesting success, especially in Grays Harbor. Increasing structure around individual nests may increase breeding success of gulls or other seabirds that experience extensive nest predation.

Key words: *Breeding success, egg loss, Glaucous-winged Gull, habitat, Larus glaucescens, L. occidentalis, Western Gull.*

Éxito Reproductivo en el Complejo *Larus occidentalis* × *glaucescens*: Influencia del Hábitat y las Características del Sitio de Anidación

Resumen. La ecología de anidación de parejas reproductivas del complejo híbrido *Larus occidentalis* × *glaucescens* fue investigada en dos localidades en la costa de Washington. En Grays Harbor, el desempeño reproductivo (en términos del tamaño de la nidada y el éxito de eclosión y emplumamiento) fue máximo en ambientes con vegetación donde los nidos estaban a mayor densidad y donde el vecino más cercano estaba separado por barreras naturales. La pérdida de huevos (presumiblemente ante gaviotas depredadoras) fue común excepto en áreas con vegetación densa. En la isla Tatoosh, la pérdida de huevos fue poco frecuente y el desempeño reproductivo fue similar en ambientes con vegetación y ambientes rocosos. Para determinar si la estructura física alrededor de los nidos en áreas abiertas influenciaba la pérdida de huevos en Grays Harbor, se construyeron cercas para excluir a los depredadores alrededor de nidos en una isla arenosa carente de vegetación. La exclusión de depredadores redujo la pérdida de huevos e incrementó el éxito de eclosión con relación a nidos con barreras naturales adyacentes (truncos de >30 cm de alto) y a nidos sin barreras naturales. Las parejas que anidan en ambientes con estructura de hábitat adecuada parecen beneficiarse en términos de una menor pérdida de huevos y un mayor éxito de anidación, especialmente en Grays Harbor. Incrementar la estructura alrededor de nidos individuales podría aumentar el éxito reproductivo de gaviotas u otras aves marinas sujetas a altos niveles de depredación de nidos.

INTRODUCTION

Colonial nesting involves costs and benefits for breeding seabirds (Wittenberger and Hunt 1985, Clode 1993). Some gull species may benefit from nesting in dense colonies via enhanced group de-

fense against predators (González-Soltís et al. 1995) or simply dilution of predator impact (Vellarde 1989). However, nesting in dense colonies can also lead to intense predation on eggs and chicks (Davis and Dunn 1976, Wilkens and Exo 1998), decreased chick growth and fledging success (Coulson et al. 1982), and epizootic outbreaks (Parsons 1975), resulting in low overall breeding success in gull colonies (Gotmark and Andersson 1984, Ewins 1991, Maccarone 1992).

Breeding performance in gulls can be influenced by nest-site selection (Bukacinski and Bu-

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kacińska 1993). High-quality nest sites often contain complex physical structure that can provide natural screens around nests and boundaries among territorial pairs (Cezilly and Quenette 1988). Extensive structure around nests can reduce predation on adults, eggs, and chicks (Burger 1974, Jehl and Chase 1987, Bukacińska and Bukaciński 1993) and promote dense nesting (Davis and Dunn 1976, Vermeer et al. 1988, but see Murphy et al. 1984). The lower predation rates in high-quality nesting habitats may result from reduced aggression (Burger 1977, Bukacińska and Bukaciński 1993) or altered patterns of parental attendance (Pierotti 1981, 1987, Morris 1987).

Members of the Western Gull \times Glaucous-winged Gull (*Larus occidentalis* \times *glaucescens*) hybrid complex breed along the Pacific Coast of North America from the Aleutian Islands in Alaska to Baja California, Mexico (Bell 1992). Both species and their hybrids breed in colonies from northern Puget Sound, Washington, to the central Oregon coast (Bell 1996). Nesting habitats of these gulls include offshore rocky islands, sea stacks, low sandy islands, and gravel spits; individual pairs nest atop buildings in coastal cities, abandoned piers, ferry docks, channel markers, dikes, and log piles at sorting yards (Speich and Wahl 1989, Verbeek 1993, Pierotti and Annett 1995). Previous studies of this hybrid complex suggested that phenotypes might associate with particular nesting habitats (Hoffman et al. 1978, Bell 1992). These habitat associations may proximately influence breeding performance and ultimately influence the long-term maintenance of the hybrid zone (Good et al. 2000).

Preliminary analyses of reproductive performance of gulls breeding on sandbar islands in Grays Harbor, Washington, suggested gulls nesting in vegetated habitats outperformed those in open sand (Good et al. 1996). To further study the association between breeding performance and habitat, I manipulated the breeding colony environment. While removing habitat structure can lead to territory abandonment in gulls (Pierotti 1981, 1982), installing structure to mimic vegetation has been used to test the predator deterrence of natural structure (Parrish and Paine 1996). Exclusion of avian and mammalian predators has been accomplished on mainland nesting areas of terns (*Sterna* spp.; Jenks-Jay 1982, Dunlop et al. 1991, Burness and Morris 1992),

plovers (*Charadrius* spp.; Melvin et al. 1992, Smith et al. 1993, Koenen et al. 1996), and ducks (Anatidae; Lagrange et al. 1995). Excluding predators from nests can thus provide a way to measure the contribution of habitat and nest-site features toward reducing nest predation and increasing breeding performance.

To determine the influence of nesting habitat and nest-site selection on nesting density and breeding success in gulls of the Western \times Glaucous-winged Gull hybrid complex, I collected data from breeding colonies in two locations within the hybrid zone from 1994–1997. For the years 1995–1997, I tested hypotheses that breeding habitats differed with respect to nesting density as measured by mean nearest-neighbor distance, quantity and quality of structure adjacent to nests (natural screens), and breeding success of gull pairs. To test the hypothesis that nonvegetative structure reduced egg predation prevalent in open habitat in Grays Harbor, I experimentally excluded predators from a small number of nests using makeshift fences.

METHODS

STUDY AREA

The study areas are located along southern coastal Washington (Fig. 1). Grays Harbor (46°57'N, 124°03'W) lies at the approximate midpoint of the Western \times Glaucous-winged Gull hybrid zone. Goose Island, Sand Island, and No Name Island are located in the northern bay of the harbor; Whitcomb Flats is located in the southern bay. The islands range from small driftwood-covered sandbars to large islands. The small islands (Goose, Whitcomb) had sparse vegetation, primarily American searocket (*Caikile edentula*) and seabeach sandwort (*Honkenya peploides*), whereas the larger islands (Sand, No Name) had dense patches of dunegrass (*Elymus mollis*) and beachgrass (*Ammophila arenaria*), with patches of Pacific willow (*Salix lucida*) and stands of common reed (*Phragmites australis*). Gulls nest in areas of either open sand or vegetation; other nesting seabird species include Double-crested Cormorants (*Phalacrocorax auritus*) and Caspian Terns (*Sterna caspia*).

Tatoosh Island (48°23'N, 124°44'W) lies just off Cape Flattery on the northwest tip of the Olympic Peninsula. The island is a complex of flat-topped rocky islets, the largest of which are covered by stands of dense, 1–2 m high salm-

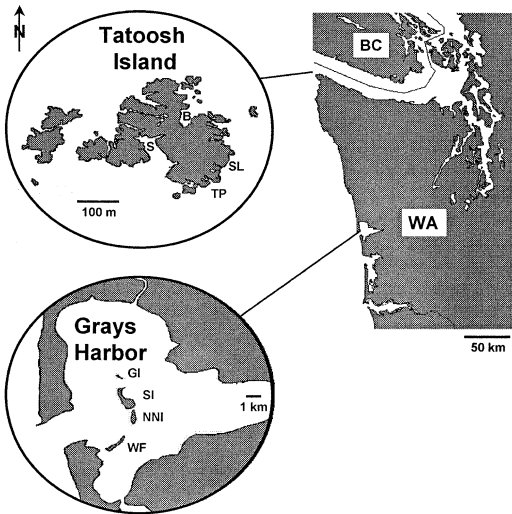


FIGURE 1. Map of Western \times Glaucous-winged Gull study locations on the outer Washington coast. On Tatoosh Island (upper inset), I worked in rock habitats at Saddle (S) and Beach (B) and vegetated habitats at Simon's Landing (SL) and Toad Point (TP). In Grays Harbor (lower inset), I worked in sand and vegetated habitats on Goose Island (GI), Sand Island (SI), No Name Island (NNI), and Whitcomb Flats (WF).

onberry (*Rubus spectabilis*). Gulls nest on rocky benches (Saddle), on areas of beachgrass and salmonberry on cliff edges (Simon's Landing, Toad Point), or adjacent to cobble beaches in protected coves (Beach; Fig. 1). Other nesting seabirds include Double-crested and Pelagic (*P. pelagicus*) Cormorants, Common Murres (*Uria aalge*), Tufted Puffins (*Fratercula cirrhata*), and Rhinoceros Auklets (*Cerorhinca monocerata*).

DATA COLLECTION AND STATISTICAL ANALYSIS

I collected data from nests on islands in Grays Harbor during the breeding seasons of 1995–1996 and on Tatoosh Island in 1996–1997. During the egg-laying period, I marked nests by attaching numbered flagging to vegetation or writing on driftwood adjacent to nests. In each nesting habitat type, I measured the distance and direction to the nearest neighboring nest. I categorized type (vegetation, driftwood, rock) and measured the angular extent (0–360°) of natural screens >30 cm in height adjacent to the nest (Cezilly and Quenette 1988) to determine if the screens blocked the view of the nearest neighbor. To test if natural screens were oriented with respect to prevailing winds, I categorized mea-

surable screens as blocking winds from one to four quadrants equal to the major compass headings. For screens facing more than one compass direction, I estimated partial values for each direction reflecting the proportion of each quadrant that the screen sheltered. I summed the values for each quadrant for nests in each study location in each year and compared them to null expected values (uniform distribution) using chi-square goodness-of-fit tests. I analyzed the influence of natural screen extent on hatching success by binning angular extent measurements into six equal categories (0–60°, 70–120°, 130–180°, 190–240°, 250–300°, 310–360°).

After the initial data collection, I checked nests twice weekly until chicks fledged in August, recording the presence of eggs and chicks as they appeared; in 1997, nest checks ended before fledging at Tatoosh Island. Eggs that I suspected were addled I gently shook to verify their inviability. From these data, I calculated the clutch size (maximum number of eggs on any visit), number of chicks hatching, number of chicks surviving to two weeks, and number of chicks fledging per nest. To produce measures of success independent of each other, I determined the percentage of viable eggs, egg survival (1 – percentage of eggs lost), hatching success (percentage of eggs producing hatchlings), 2-week-old success (percentage of eggs producing 2-week-old chicks), and fledging success (percentage of eggs producing fledglings) for each nest. To track individuals, I banded chicks with United States Fish and Wildlife Service aluminum bands when they reached 100 g (ca. 5 days).

To test the influence of structure near the nest, I conducted an exclusion experiment during the breeding season of 1996 on Whitcomb Flats, an unvegetated 5-ha sandbar in the southern bay of Grays Harbor. I selected 81 nests with at least one egg and categorized them as one of two treatments, *natural screen* and *no screen*, based on the presence of structure adjacent to the nest cup. I established a third treatment, *exclusion fence*, at a randomly selected subset of no-screen nests. The natural-screen treatment had structure (usually driftwood logs) >30 cm high adjacent to the nest cup, while the no-screen treatment lacked natural screens. The exclusion fence treatment consisted of predator exclusion fences placed around nests that lacked natural screens. Extreme tides destroyed some nests in all treat-

TABLE 1. Frequency and characteristics of natural screens around Western \times Glaucous-winged Gull nests in sand, rock, and vegetated habitats at Grays Harbor and Tatoosh Island, Washington, 1995–1997.

	Grays Harbor 1995–1996		Tatoosh Island			
	Sand	Vegetated	1996		1997	
			Rock	Vegetated	Rock	Vegetated
<i>n</i> tests	328	316	30	18	61	48
<i>n</i> screened (%) ^a	98 (30)	306 (97)***	24 (80)	16 (89)	38 (62)	47 (99)***
<i>n</i> with blocked view (%) ^{a,b}	36 (37)	242 (79)***	13 (54)	11 (69)	20 (53)	43 (91)***
Screen extent (mean \pm SE) ^c	82 \pm 6	234 \pm 5***	135 \pm 15	240 \pm 24***	135 \pm 10	292 \pm 11***

*** $P < 0.001$.

^a Differences between habitats (within years at Tatoosh Island) tested using chi-square tests.

^b Percentage calculated as number of blocked-view nests/number of screened nests.

^c Measured in angular degrees around nest, for nests with screens only. Differences between habitats (within years at Tatoosh Island) tested using *t*-tests.

ments; thus 64 nests (16 natural screen, 38 no screen, 10 exclusion fence) were included in the final analysis.

I constructed exclusion fences from small-diameter (2–4 cm) driftwood pushed into the sand around the nest perimeter, forming a 30-cm-high barrier. To mimic the average screen extent in vegetated habitats, I placed sticks at 25-cm intervals, creating a barrier 270° around the nest circle, and aligned fence openings with paths commonly used by the breeding pair. I collected data on egg loss and breeding success at all treatments during twice-weekly visits to the island from mid-May to mid-August 1996.

For data on nearest neighbor distance, angular extent of natural screens, and reproductive success, I used parametric analyses where variances were homogeneous and Kruskal-Wallis ANOVA and Mann-Whitney *U*-tests where variances were heterogeneous (SYSTAT 2000). For each location, I pooled data from both years, except where differences between years precluded combining them for analyses. Data are presented as means \pm SE.

RESULTS

NEST-SITE CHARACTERISTICS

In 1995–1996, data collected from 645 active nests (nests with ≥ 1 egg) in Grays Harbor revealed that nests in vegetated habitat were more densely spaced than in sand habitat. Nearest-neighbor distances were significantly greater at nests in sand habitat (6.1 \pm 0.4 m, $n = 330$) than at nests in vegetated habitat (4.0 \pm 0.2 m, $n = 315$; $U = 16\,080$, $P < 0.001$). Natural screens formed considerable barriers between

breeding pairs in vegetated habitat. Structure around nests in vegetated habitat was three times more frequent and ten times more extensive than in sand habitat (Table 1). For nests with natural screens, the direction of screens (90 west, 90 south, 89 east, 89 north) was not biased toward prevailing westerly and southerly winds ($\chi^2_3 = 0.3$, $P > 0.5$).

At Tatoosh Island in 1996, data collected from 48 active nests revealed that nest-site characteristics differed between habitats to a lesser degree than in Grays Harbor. Nearest-neighbor distances were similar for nests in rock habitat (1.9 \pm 0.1 m, $n = 30$) and nests in vegetated habitat (2.3 \pm 0.2 m, $n = 18$; $t_{46} = 1.8$, $P = 0.08$). Structure was more extensive around nests in vegetated habitat (Table 1).

In 1997, data collected from 109 active nests revealed that nests in vegetated habitat had more extensive screens than nests in rock habitat (Table 1). Nearest-neighbor distances, while greater than in 1996, were again similar for nests in rock habitat (2.6 \pm 0.2 m, $n = 63$) and nests in vegetated habitat (3.0 \pm 0.2 m, $n = 44$; $t_{105} = 1.4$, $P = 0.19$). The distribution of screens in 1996 (12 west, 8 south, 13 east, 6 north) was not biased toward the prevailing westerly and southerly winds ($\chi^2_3 = 3.4$, $P = 0.30$), nor was the distribution of screens in 1997 (27 west, 14 south, 18 east, 23 north; ($\chi^2_3 = 2.8$, $P = 0.40$).

REPRODUCTIVE SUCCESS

In Grays Harbor in 1995, clutch size was greater in vegetated habitat (1.9 \pm 0.1, $n = 147$) than in sand habitat (1.3 \pm 0.1, $n = 178$; $U = 7506$, $P < 0.001$). In 1996, clutch size was again great-

er in vegetated habitat (2.2 ± 0.1 , $n = 169$) than in sand habitat (1.9 ± 0.1 , $n = 152$; $U = 10\,594$, $P = 0.05$). The proportion of nests with two-egg and three-egg clutches was greater in vegetated habitat than in sand habitat in both years (Table 2). At Tatoosh Island, clutch size in 1996 was similar in vegetated habitat (2.3 ± 0.2 , $n = 18$) and rock habitat (2.7 ± 0.1 , $n = 30$; $U = 356$, $P = 0.09$). In 1997, clutch size was greater in vegetated habitat (2.7 ± 0.1 , $n = 45$) than rock habitat (2.5 ± 0.1 , $n = 58$; $U = 10\,505$, $P = 0.04$).

Mean egg viability (the percentage of viable eggs per clutch) showed no consistent association with nesting habitat. In Grays Harbor, nests in sand habitat had a greater percentage of viable eggs than nests in vegetated habitat in 1995 ($U = 38\,486$, $P = 0.04$) but not in 1996 ($U = 7670$, $P = 0.16$; Fig. 2). At Tatoosh Island, the percentage of viable eggs was not consistent between years, nor was it consistent with the patterns in Grays Harbor. Nests in rock habitat had a greater percentage of viable eggs per clutch than nests in vegetated habitat in 1996 ($U = 240$, $P = 0.03$) but not 1997 ($t_{88} = 0.2$, $P = 0.8$; Fig. 3).

The association of chick production with nesting habitat was not consistent between locations. Overall chick production in Grays Harbor was greater in 1996 than in 1995, and hatching success was greater in vegetated habitat than in sand habitat in 1995 ($U = 31\,915$, $P < 0.001$) and 1996 ($U = 6048$, $P < 0.001$; Fig. 2). Hatching success was also consistently greater at nests with more extensive natural screens in 1995 (Kruskal-Wallis $H = 36.6$, $P < 0.001$) and 1996 (Kruskal-Wallis $H = 50.1$, $P < 0.001$). Hatching production at Tatoosh Island was similar at nests in rock and vegetated habitat (Table 2) but was consistently greater than in Grays Harbor. Hatching success at Tatoosh Island did not differ between habitats in 1996 ($t_{46} = 0.9$, $P = 0.4$) or 1997 ($t_{74} = 0.4$, $P = 0.6$; Fig. 3), nor was it greater at nests with more extensive natural screens in 1996 ($H = 4.0$, $P = 0.5$) or 1997 ($H = 1.8$, $P = 0.9$).

The association of 2-week-old chick and fledgling production with nesting habitat was also not consistent between locations. Overall fledgling production in Grays Harbor was greater in 1996 than in 1995. Nests produced more fledglings in vegetated habitat in both years (Table 2), and fledging success in Grays Harbor was

greater at nests in vegetated habitat in 1995 ($U = 33\,267$, $P < 0.001$) and 1996 ($U = 5964$, $P < 0.001$; Fig. 2). At Tatoosh Island, production of fledglings in 1996 and production of 2-week-old chicks in 1997 did not differ between habitats (Table 2). Two-week-old success ($t_{45} = 0.05$, $P = 0.9$) and fledging success ($t_{40} = 1.7$, $P = 0.1$) did not differ between rock and vegetated habitat in 1996, and 2-week-old success did not differ between habitats in 1997 ($t_{59} = 0.6$, $P = 0.5$; Fig. 3).

EXCLUSION EXPERIMENT

Exclusion fences ($n = 10$) reduced egg loss and increased breeding success relative to nests with either natural screens ($n = 16$) or no screens ($n = 38$). Percent egg survival was significantly greater at experimental nests than at either natural-screen or no-screen control nests ($F_{2,59} = 6.5$, $P < 0.01$, Tukey HSD test, $P < 0.05$). Percent egg survival at experimental nests ($54 \pm 15\%$) was significantly greater than at no-screen and natural-screen nests combined ($14 \pm 4\%$; $t_{59} = 3.5$, $P = 0.001$; Fig. 4). Hatching success was greater and more variable at experimental nests ($38 \pm 17\%$) than at control nests ($13 \pm 4\%$; $t_{59} = 2.1$, $P = 0.04$, Fig. 4). Fledging success was not significantly greater at experimental nests ($29 \pm 16\%$) than at control nests ($8 \pm 3\%$; $U = 145$, $P = 0.06$; Fig. 4). While a greater proportion of control nests failed to produce any chicks (78%) than did experimental nests (50%), the distribution of failed nests in the treatments did not differ significantly from expected values ($\chi^2_2 = 2.9$, $P = 0.2$).

DISCUSSION

Breeding success was significantly associated with nesting habitat and nest-site characteristics at one of two disparate breeding locations of the Western Gull \times Glaucous-winged Gull hybrid complex. In Grays Harbor, extensive differences in reproductive output were consistently associated with differences in nest-site characteristics between habitats. Pairs nesting in vegetated habitat were closely spaced, had extensive natural screens, and produced more chicks than did pairs nesting in sand habitat. At Tatoosh Island, nest-site characteristics did not consistently differ between habitats, and reproductive output showed little association with habitat or habitat characteristics. Pairs nesting in vegetated habitat generally had more extensive natural screens

TABLE 2. Breeding performance of Western \times Glaucous-winged Gulls in sand, rock, and vegetated habitats of Grays Harbor and Tatoosh Island, Washington. Columns indicate distributions of eggs or chicks in nests and mean numbers of eggs, hatchlings, or fledglings produced per nest.

	Grays Harbor												Tatoosh Island											
	Sand						Vegetated						Rock						Vegetated					
	0	1	2	3	mean	0	1	2	3	mean	0	1	2	3	mean	0	1	2	3	mean				
Clutch size																								
1995	129	37	12	12	1.3	48	60	38	38	1.9***														
1996	55	52	45	45	1.9	34	69	65	65	2.2**	1	7	22	22	2.70	4	5	9	9	2.30				
1997											7	15	36	36	2.50	1	8	36	36	2.70*				
Hatchlings																								
1995	172	5	1	0	0.04	116	15	13	3	0.33***														
1996	119	11	12	3	0.30	76	19	31	8	0.79***	5	8	7	10	1.73	5	3	6	4	1.50				
1997											11	16	13	8	1.38	7	13	10	8	1.50				
2-week-old chicks (1997)											7	12	13	5	1.43	6	7	7	4	1.37				
Fledglings																								
1995	173	0	1	0	0.01	127	9	2	2	0.14***														
1996	119	8	5	1	0.16	78	16	20	5	0.60***	7	7	11	4	1.41	6	3	4	0	0.92				

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; Mann-Whitney U -test between habitats within years.

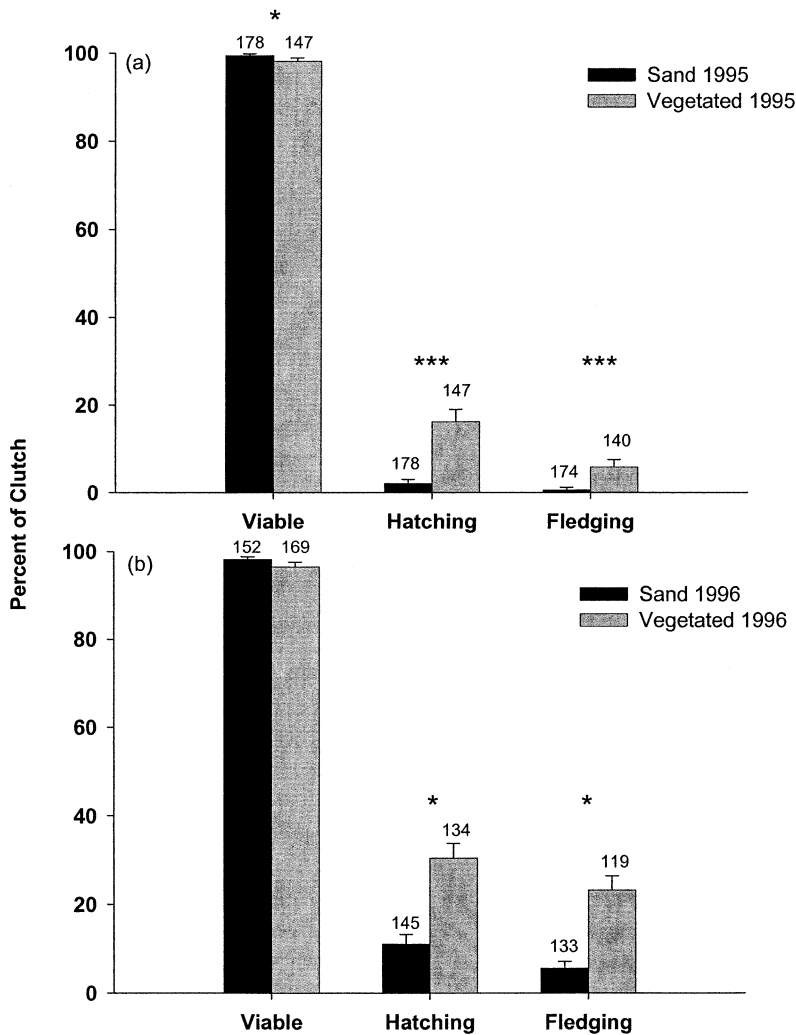


FIGURE 2. Mean \pm SE percentage of viable eggs per clutch, hatching success, and fledging success in sand and vegetated habitats in Grays Harbor in (a) 1995 and (b) 1996. Sample sizes (nests) appear above bars; * $P < 0.05$; *** $P < 0.001$.

than did pairs in rock habitat; however, pairs in both rock and vegetated habitats nested close together (at half the distance of Grays Harbor pairs) and had similar chick production.

Differences in reproductive success between habitats in Grays Harbor, particularly hatching and fledging success, were quite likely the result of extensive egg predation by gulls, which I observed regularly during the study. Opportunistic predation was widespread; while few individual gulls were egg specialists, nest-site sampling showed that eggs formed a small but consistent part of the diet of breeding pairs, especially in

sand habitat (Ellis 1997). Individuals loafing in peripheral areas were likely additional predators. Nonbreeding individuals or failed breeders represent predation threats (Pierotti and Annett 1995); however, I rarely observed subadult and juvenile gulls within the study colonies. At Tatoosh Island, egg loss attributable to predation was less prevalent overall, and hatching success in vegetated and rock habitats reflected this. In Grays Harbor, I found additional evidence of nest predation by known egg predators including Bald Eagles (*Haliaeetus leucocephalus*; Hayward et al. 1977, Thompson 1989), Common

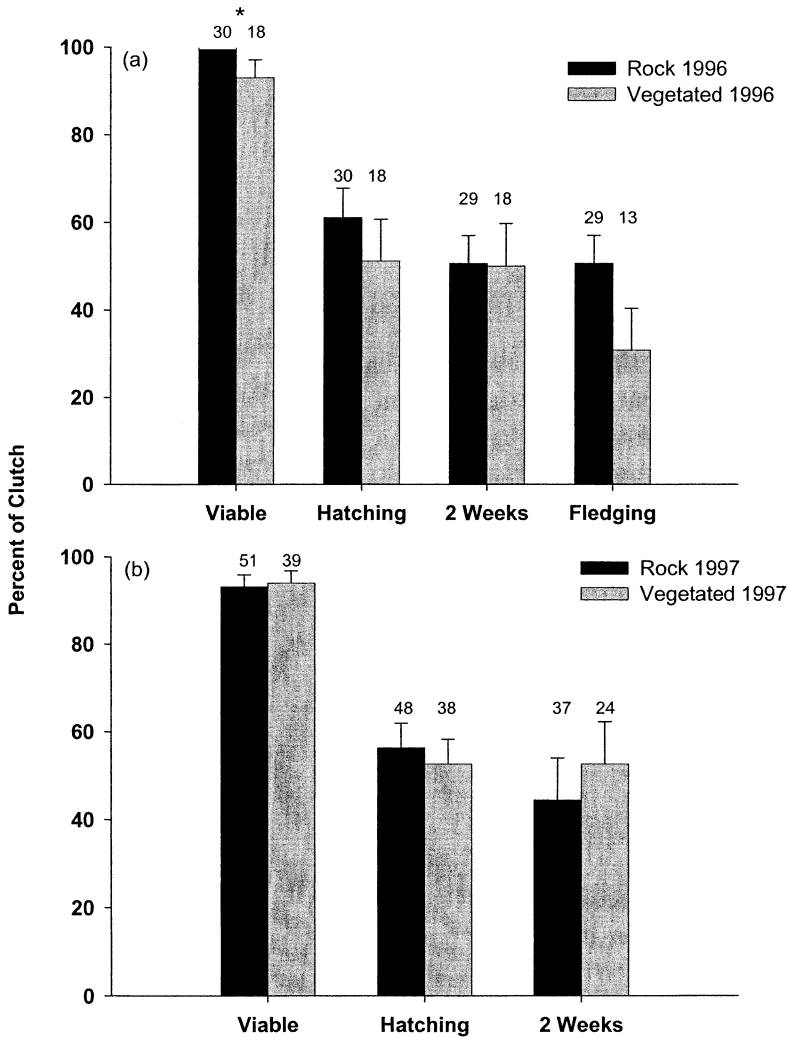


FIGURE 3. Mean \pm SE percentage of viable eggs per clutch, hatching success, 2-week success, and fledging success in rock and vegetated habitats at Tatoosh Island in (a) 1996 and (b) 1997. Sample sizes (nests) appear above bars; * $P < 0.05$.

Ravens (*Corvus corax*; Baird 1990), and Northwestern Crows (*Corvus caurinus*; Verbeek 1982), but this occurred rarely. I observed no evidence of egg predation by mammals.

Whereas eagles were rare egg predators, the disturbances they caused were commonplace at both locations. Generally, when eagles flew over colonies, adult gulls flew above their nests en masse and gave alarm calls. Gulls took advantage of such disturbances, particularly in open sand habitat in Grays Harbor. Landing at unprotected nests, they would swallow eggs whole, crack them open and eat them at the nest, or fly

to a nearby spot and eat them. Disturbances from eagles can devastate cormorant colonies through predation by crows and gulls (Verbeek 1982), and increasing numbers of eagles along coastal Washington (Galusha and Hayward 2002) may have profound influences on seabird colonies with abundant open habitat.

At Tatoosh Island, eagle disturbances were frequent and intense, but disturbances of gull colonies did not lead to widespread egg predation by other gulls or to reproductive failure, even in the relatively open rock habitats (pers. obs.). Instead, gull alarm calls in response to ea-

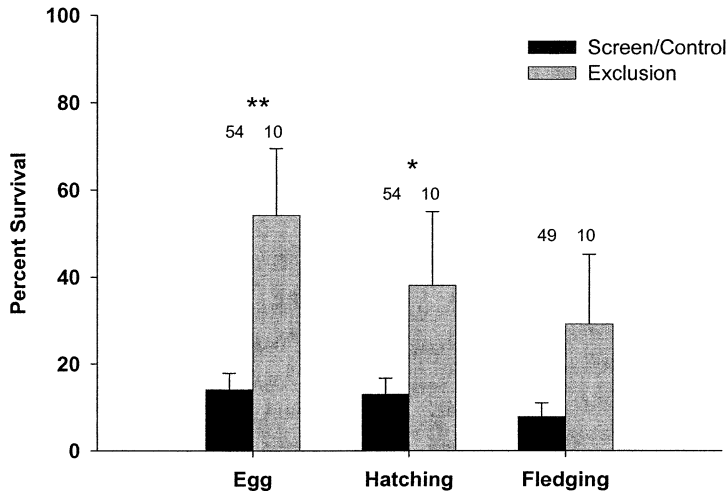


FIGURE 4. Egg survival (mean percentage of eggs surviving per clutch \pm SE), hatching success (mean percentage of eggs hatching chicks \pm SE) and fledging success (mean percentage of eggs producing fledglings \pm SE) at exclusion-fence nests and natural-screen and no-screen control nests combined; * $P < 0.05$; ** $P < 0.01$.

gle disturbances flushed breeding Common Murres from their nests, which led to predation of murre eggs by gulls and crows (Parrish 1995, Parrish and Paine 1996). Numbers of eagles and eagle disturbances in the vicinity of Tatoosh Island have increased throughout the 1990s (Parrish 1995, Parrish and Paine 1996), resulting in highly variable breeding success in murres (Parrish et al. 2001); juvenile eagle predation on gull chicks has been prevalent in some years since 1998 (J. Parrish, pers. comm.).

Lower levels of egg loss in heterogeneous habitat (vegetation in Grays Harbor; both habitats at Tatoosh) suggest that physical structure around nests was important to breeding success at colonies that experience frequent levels of disturbance. In Grays Harbor, rates of egg loss were highest where vegetation was absent and structure around nests minimal (sand habitats). The extent of egg and chick mortality in gulls is often related to nesting habitat type (Burger 1974, Pierotti 1982) and the extent or distribution of vegetation (Jehl and Chase 1987, Bukacińska and Bukaciński 1993, Bukaciński and Bukacińska 1993).

Heterogeneous habitat in both locations created physical structure around nests (Burger and Gochfeld 1981). Natural screens usually blocked the view of the nest from the nearest neighbor, and such reduced visibility of neighboring pairs is known to reduce the frequency of territorial

and aggressive behaviors (Burger 1977, Bukacińska and Bukaciński 1993). Although not as heterogeneous as vegetation, rock habitat may provide structure that allows gulls to nest densely (Davis and Dunn 1976, Vermeer et al. 1988). Herring Gulls (*L. argentatus*) in the Gulf of Maine nest in dense colonies on the rocky edges of islands. On Appledore Island in Maine, Herring Gull pairs nest more densely in heterogeneous rock habitat than in the vegetated interior, where they have fewer aggressive interactions with Great Black-backed Gulls (*L. marinus*; TPG, unpubl. data), and their breeding success is greater (Pierotti and Good 1994, Good 1998a).

Higher nesting densities in areas of habitat heterogeneity appeared to exert a positive, rather than a negative influence. In high-density habitats (vegetation in Grays Harbor; rock and vegetation at Tatoosh Island), eagles were intensely mobbed by large numbers of gulls; in low-density habitats (sand), small numbers of gulls spent a lot of time in the air chasing eagles from the area (pers. obs.). Such mobbing potential may reduce the influence of raptors. Small, low-density subcolonies of Audouin's Gulls (*Larus audouinii*) are subject to intense predation by Peregrine Falcons (*Falco peregrinus*) and Yellow-legged Gulls (*L. cachinnans*; Oro and Martínez-Vilalta 1994, González-Soltf's et al. 1995). Likewise, high-density areas of California Gull

(*Larus californicus*) colonies experience reduced predation by Great Horned Owls (*Bubo virginianus*; Jehl and Chase 1987). Thus, eagles in Grays Harbor may have concentrated on low-density sand habitats, where mobbing potential is lower.

In this study, intense levels of neighbor interactions and nest predation, which are usually associated with high-density areas (Hunt and Hunt 1976, Spear and Anderson 1989, Kilpi 1995, but see Jehl 1994), appeared to have been more the case in low-density sand habitats. Pairs in open sand may have spent more time defending their larger territories, which is known to lead to reductions in breeding success (Ewald et al. 1980). By contrast, nests in stands of the densest vegetation in Grays Harbor were often located at the end of tunnels up to 4 m long into the reeds; rather than spending time interacting with neighbors in territorial disputes, gulls loafed in nearby open spaces (pers. obs.). Open sand habitat may thus be suboptimal relative to vegetated habitat. Not only were clutch sizes smaller, but also the number of days after 1 June that α -eggs (first eggs recorded) hatched in sand habitat (median = 52 days) was much later than in vegetated habitat (median = 21 days) in 1995. In 1996, the contrast in median hatching dates was not as strong but was similar in direction (33 days in sand habitat vs. 28 days in vegetated habitat, Good 1998b). Nesting in centrally located vegetated habitat or nesting earlier may contribute to the greater breeding success evidenced in vegetated habitat (Coulson 1968, Parsons 1975, Parsons et al. 1976). Younger or less experienced individuals may also elect or be relegated to open sand habitats (Cairns 1992), contributing to differences in breeding success between habitats.

Breeding success varied between years, particularly in Grays Harbor. Such variation and its effect on phenotypes have been attributed to interannual variation in the marine environment (Bell 1997). In Grays Harbor, breeding success was greater in 1996 than 1995, although El Niño-Southern Oscillation (ENSO) indices were similar for both years; while ENSO indices in 1997 were much greater than in 1996, breeding success did not differ between years at Tatoosh Island. Bell (1997) attributed this to a year lag in effect on gull diet, a possibility suggested by the normal breeding success of Common Murres on Tatoosh Island during the 1997 El Niño (J.

Parrish, pers. comm.). Bell (1997) also hypothesized that Western Gulls and hybrids experienced reciprocal shifts in reproductive performance based on oceanographic conditions, with Glaucous-winged Gulls doing poorly in all years. However, Glaucous-winged Gulls had the best, not the worst, breeding performance overall (Good et al. 2000), contrary to the patterns found by Bell (1997). If interannual variability in ocean conditions does play a role, it did not appear to drive patterns in breeding success during this study.

The exclusion experiment demonstrated that restricted access to individual gull nests in sand habitat reduced egg predation by mimicking the protection afforded to breeding gulls in heterogeneous habitat. Egg-loss levels and hatching success at experimental nests approached those observed in vegetated habitats throughout Grays Harbor, and egg loss and hatching success at control nests paralleled those in sand habitat throughout Grays Harbor. Fencing individual nests (Melvin et al. 1992) or large areas (Smith et al. 1993) can increase hatching success of plovers, and fencing larger open areas reduces nest predation in plovers and terns (Koenen et al. 1996) as well as ducks (Lagrange et al. 1995). Fences designed to keep gull chicks in their own territories increase predation by preventing chicks from escaping from aerial predators (J. Galusha, pers. comm.); however, the makeshift exclusion fences in this study did not restrict chick movement or appear to increase chick predation relative to controls. On rocky islands, erecting dense natural or artificial vegetation on cliff-top colonies protects eggs of Common Murres from predation by gulls and crows (Parrish 1995, Parrish and Paine 1996).

Exclusion fences did not, however, fully mimic dense vegetation. Although egg loss was reduced in open habitat, it was not eliminated, and subsequent fledging success was variable and only marginally higher than in control nests. The experiment did have low sample sizes and high variance, masking any possible effects of the exclusion-fence treatment, especially on chick survival to fledging. I also observed wandering chicks being attacked by congeners, suggesting that driftwood stick fences are probably insufficient chick shelters. A pilot study to assess the effect of wooden chick shelters in a small area of sand habitat on Sand Island suggested that chicks used shelters near the nest (TPG, unpubl.

data). Structure that is much more significant than driftwood fences may thus be necessary to increase chick survival (Jenks-Jay 1982, Burness and Morris 1992).

Among the costs of colonial breeding in seabirds, predation is thought to be one of the most important (Wittenberger and Hunt 1985, Clode 1993). For many gull species, nesting habitat and nest-site microhabitat influence egg and chick predation and subsequent breeding success. This study demonstrated through observational and experimental evidence that heterogeneous habitats provided structure around nests, reducing egg loss that was presumably due to other gulls. Adding artificial or natural structure may be a useful technique for protecting nests of gull species endangered or threatened by predation by other gulls, such as of Audouin's Gull (Castilla 1995, Oro 1996). In circumstances similar to those along this coast, where various breeding habitats are available for colonial seabirds, survival of eggs and chicks may be strongly influenced by interactions between habitat characteristics, predator abundance and behavior, and behavior of breeding pairs.

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