MATING PATTERNS AND BREEDING SUCCESS IN GULLS OF THE *LARUS GLAUCESCENS-OCCIDENTALIS* COMPLEX, PROTECTION ISLAND, WASHINGTON, USA

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ABSTRACT—Glaucous-winged Gulls (*Larus glaucescens*) and Western Gulls (*Larus occidentalis*) are found along the Pacific Coast of North America. Where their breeding ranges overlap in Oregon and Washington they hybridize, producing a continuum of phenotypic variation. Whereas most colonies containing these hybrids are found on islands along the coast, several, including a large colony at Protection Island National Wildlife Refuge, WA, USA, are located in the Salish Sea. In 2010, we scored the phenotypes of 81 gull pairs at the Protection Island colony using an index based on plumage melanism and bare-part coloration. We also monitored the breeding success of these pairs. Gulls from the entire range of phenotypes in the *L. glaucescens-occidentalis* complex bred on the colony, although most gulls appeared more like *L. glaucescens*. Significant assortative mating based on colorimetric phenotype occurred on the colony, but a low number of *L. occidentalis*-type pairs appeared primarily responsible for this trend. Although the mass of the 3rd egg in the clutch was significantly smaller for pairs with increasingly *L. occidentalis*-like males, we observed no significant difference in hatching success or clutch size across the range of phenotypes.

Key words: assortative mating, breeding success, egg size, Glaucous-winged Gull, hybridization, *Larus glaucescens*, *Larus occidentalis*, mating patterns, Protection Island, Washington, Western Gull

Hybridization between Glaucous-winged Gulls (*Larus glaucescens*) and Western Gulls (*Larus occidentalis occidentalis*) in the Pacific Northwest, USA, has been noted since the early 20th century (Dawson 1908). *Larus glaucescens* also is known to hybridize with members of 3 other gull species in the North Pacific and Bering Sea region: Herring Gulls (*Larus argentatus*; Williamson and Peyton 1963), Glaucous Gulls (*Larus hyperboreus*; Strang 1977; McCaffery and others 1997), and Slaty-backed Gulls (*Larus schistisagus*; Howell and Dunn 2007). By contrast, *L. occidentalis* is not known to hybridize with any species other than *L. glaucescens*. The presence of reproductively viable offspring from naturally occurring *L. glaucescens-occidentalis* hybrid pairs suggests that they represent a single species according to the biological species concept (Mayr 1942). However, factors noted by previous investigators such as the presence of assortative mating based on colorimetric characters and the limited size of the hybrid zone support the current classification of *L. glaucescens* and *L. occidentalis* as separate species (Hoffman and others 1978; Bell 1996; Good and others 2000).

The *L. glaucescens-occidentalis* hybrid zone occurs along a transition between 2 marine ecosystems, the first characterized by fjords and estuaries and the second by the California Current and coastal upwelling (Bell 1996). *Larus glaucescens* breeds from western Alaska south along the Pacific Coast to northern Oregon and has adapted to the 1st ecosystem; by contrast, *L. occidentalis* breeds from northern Washington to Baja California, although breeding has been reported in southern British Columbia (Pearse 1946; Scott 1971), and has adapted to the 2nd ecosystem (Bell 1996; Howell and Dunn 2007).

The relationship between the ecotone and the hybrid zone has been of particular interest, as it potentially explains why hybrids thrive in coastal Oregon and Washington (Bell 1996;

TABLE 1. Hybrid index used to score individual birds. The character score (CS) was used for statistical analyses. Kodak values (KV) were recorded while on the colony. Note that whereas character scores for back and wingtips are rounded to 1 decimal place in this table, we used the full values in statistical analyses.

Back		Wingtips		Orbital ring		Beak		Iris	
KV	CS	KV	CS	Color	CS	Color	CS	Color	CS
4	1	5	1	Pink	1	Dull Yellow	1	Dark	1
5	2.3	6	1.6	Pink-Yellow	5.5	Yellow	5.5	Medium	5.5
6	3.6	7	2.3	Yellow	10	Yellow-Orange	10	Light	10
7	4.9	8	2.9						
8	6.1	9	3.6						
9	7.4	10	4.2						
10	8.7	11	4.9						
11	10	12	5.5						
		13	6.1						
		14	6.8						
		15	7.4						
		16	8.1						
		17	8.7						
		18	9.4						
		19	10						

Good and others 2000). Good and others (2000) argued that *L. glaucescens-occidentalis* hybrids outcompete parental species in the ecotone by combining adaptive behaviors of the parental species. They found, as did Hoffman and others (1978), that pairs with hybrid members had greater reproductive success than pairs without a hybrid member. In contrast, Bell (1997) found that pairs with at least 1 *L. occidentalis* member experienced greater reproductive success than other pair combinations in the hybrid zone.

We conducted our study at Protection Island National Wildlife Refuge, WA, which is located in the Salish Sea near the northern end of the *L. glaucescens-occidentalis* hybrid zone (Bell 1996). Earlier comparisons of colorimetric variability and reproductive success in gulls of the *L. glaucescens-occidentalis* complex have been limited to sites on the outer coast (Hoffman and others 1978; Bell 1997; Good and others 2000). Previous study of colorimetric variability of this gull complex on Protection Island has been limited to work by Bell (1996). He collected 17 gulls on Protection Island and determined their phenotypes; however, Bell did not measure the reproductive success of these birds. Thus, our work provides the first large-scale description of colorimetric variability in gulls of the *L. glaucescens-occidentalis* complex on Protection Island, and the first comparison between colorimetric phenotype and breeding success of these gulls in the Salish Sea. We tested the null hypotheses that no assortative mating occurred among the gulls, and that there was no relationship between reproductive success and colorimetric phenotype.

METHODS

To quantify gull phenotypes we used a hybrid index designed specifically for members of the *L. glaucescens-occidentalis* complex, based on work by Bell (1996, 1997). Before Bell developed a hybrid index, he measured both morphometric and colorimetric characters of *L. glaucescens*, *L. occidentalis*, and hybrids on breeding colonies along the west coast of North America from Alaska to Baja California. He did not find significant morphometric differences between parental species and hybrids; however, he did find significant colorimetric differences. Thus, in forming his hybrid index, Bell included only colorimetric characters. In following with Bell's work, we included 5 colorimetric characters in our hybrid index: back (mantle plus scapulars) and wingtip melanism, and orbital ring, beak, and iris color (Table 1). A lower hybrid index corresponded to a more *L. glaucescens*-like phenotype; a higher hybrid index corresponded to a more *L. occidentalis*-like phenotype. In contrast to several previous studies that used the Munsell 37-step neutral value scale, we quantified plumage melanism using the 19-step Kodak Gray Scale because of its accessibility, ease of use in the field, and application to gull plumage by Howell and Dunn (2007). Because methodologies described by previous investigators lack precise details in how to score plumage melanism with a gray scale, it could be misleading to compare results with those in previous studies, even if using the Munsell scale. The shades of the Kodak Gray Scale range from very pale gray (1) to black (19). Although the back and wingtips of adult gulls often show slight bluish or brownish tones, respectively, the shades can still be approximated with a neutral gray scale.

To quantify the bare-part coloration we used a 3-point scale. Orbital ring was recorded as ''1'' when dull to bright pink; ''2'' when both pink and yellow, even if one of these colors was limited to a few nodules of the orbital ring; and ''3'' when solid yellow or yellow with some orange nodules. Beak color was recorded as ''1'' when dull, pale yellow; ''2'' when medium to bright yellow; and ''3'' when yellow-orange to orange. Iris color was recorded as ''1'' when dark brown to black, with little pupil to iris contrast; ''2'' when medium brown or pale with large brown splotches; and ''3'' when pale to yellowish with no or minimal dark flecking.

Our study site was a breeding colony of gulls of the *L. glaucescens-occidentalis* complex located on Violet Point, Protection Island National Wildlife Refuge (UTM: Zone 10U, 506132 E, 5330516 N, WGS84), Jefferson County, WA. On 24, 25, 27, and 28 June 2010, 2 of us (AEM and LCM) independently used the hybrid index to quantify phenotypes in a study area previously set up to monitor gull reproductive success. We worked when the sky was overcast, avoiding sunny and low-angle light conditions, which could variably affect the appearance of the gulls through shadows, backlighting, or washing out of color (Howell and Dunn 2007). Average feather shade and bare-part coloration were determined at close quarters, mostly within 3 m, using naked-eye observations useful for comparing individuals, binoculars, and a Nikon Fieldscope 82mm ED.

We determined the sex of each gull by noting features such as bill length, bill depth, head shape, and body size, often in direct comparison with a mate, with females being the smaller of the 2 sexes in gulls (Pierotti 1981; Bell 1996; Howell and Dunn 2007). To ensure that we did not mix up pairs or members of pairs, we only scored birds that were either attending a marked nest, in close proximity to such a nest, or engaged with a known individual in courtship behavior. After identifying the sex of a focal bird, we independently assessed all 5 characters in the hybrid index. If our respective determinations differed for bare-part scores, we discussed them until reaching consensus; however, if our determinations differed for back and wingtip scores, we took their average.

It is possible that some unconscious bias occurred while scoring these birds because they were not scored in isolation from each other. However, we believe that the presence of nearby birds, despite the risk of bias, was important for us to best describe their appearance. The scoring process was not a formulaic one, as each bird had different amounts of feather wear and color variation within feather tracts and bare parts. It was often very helpful to compare the appearance of multiple birds before assigning scores. For bare-part characters, which were scored based on descriptive categories, this comparison process was especially useful. Our protocol of having 2 observers independently score all features of the birds was an important protection against bias, and we are unaware of a previous study of this kind that has taken such a precaution.

To monitor reproductive success, we placed numbered stakes adjacent to each nest in our study area the day the 1st egg appeared in that nest. We labeled each egg of each nest according to its order of appearance, and monitored all nests and eggs each evening from 25 May through 19 July 2010 to determine egg fate. On the day an egg was laid, we measured its mass to the nearest tenth of a gram using a 400-g capacity Ohaus Scout Pro SP401 portable electronic balance.

To eliminate arbitrary weighting of the 19-step Kodak values compared to bare-part coloration values on the 3-point scale, we adjusted all values to a 10-point scale, generating character scores for use in statistical analyses. Thus, the lowest observed back value on the Kodak scale (4) was converted to 1, and the highest back value (11) was converted to 10. All intervening Kodak values were spaced evenly between 1 and 10. The same conversions were done for wingtip values (Kodak scale range 5–19) and bare-part coloration values (arbitrary range 1–3). It is important to note that on the 10-point scale the same character scores for back and wingtips do not correspond to the same Kodak values.

For analyses of multiple characters, we summed the beak, orbital ring, and iris scores to generate the bare-part score, and we summed the back and wingtip scores to generate the back-wingtip score. We defined the hybrid index as the sum of the bare-part score and 2 times the back-wingtip score. The back-wingtip score was doubled because plumage melanism is considered the best way to visually distinguish hybrids from pure birds (Bell 1996). Hybrid indices for the male and female in a pair were summed to generate the pair hybrid index.

We collected complete hybrid index data for 81 gull pairs. Pairs were selected for scoring on the basis of availability during data collection. Using Pearson correlation analyses we tested the degree of assortative mating and the relationship between hybrid index and egg mass. The correlations between hybrid index and mass of the 3rd egg in the clutch were carried out for 49 of 81 pairs, because the remaining nests did not contain a 3rd egg. Phenotypic differences between the 81 males and 81 females were analyzed using the Mann-Whitney *U* test.

To test whether *L. glaucescens*-like gulls had greater breeding success than *L. occidentalis*-like gulls, we regressed clutch size and hatching success against the male, female, and pair hybrid indices using ordinal logistic regression (MATLAB 7.13). The resulting odds ratios (*OR*s) quantify the change in the odds of having a greater outcome (clutch size or hatching success) resulting from a change *c* in the independent variable (hybrid index; Hosmer and Lemeshow 2000). To test whether hybrid gulls had greater breeding success than parental species, we first adjusted male and female hybrid indices by taking their absolute difference from the midpoint of the range of observed hybrid indices (40.75). We adjusted the pair hybrid indices by taking their absolute difference from 2 times the midpoint. Thus, a higher adjusted hybrid index corresponded to a more parental-like phenotype, whereas a lower adjusted hybrid index corresponded to a more hybrid-like phenotype. We then regressed clutch size and hatching success against the male, female, and pair adjusted hybrid indices using ordinal logistic regression. Clutch-size data were obtained and analyzed for 81 pairs, while hatching-success data were obtained and analyzed for 69 pairs. We defined clutch size as the total number of eggs laid/nest, and hatching success as the number of eggs hatched/nest. The significance level chosen for statistical tests was $\alpha = 0.05$.

RESULTS

The appearance of the gulls on the Violet Point colony tended towards the *L. glaucescens* phenotype, although a wide range of colorimetric phenotypes were present (Fig. 1). Average female wingtip score, iris score, and hybrid index were significantly higher (indicating more like *L. occidentalis*) than corresponding male scores (Table 2). Male hybrid index and female hybrid index were significantly correlated (Fig. 2). The correlation between male back-wingtip score and female back-wingtip score was also significant ($r = 0.250$, $df = 79$, $P = 0.025$).

Correlations between various phenotypic characters and the masses of the 1st and 2nd eggs in the clutch were not significant. However, male back-wingtip score was significantly negatively correlated with the mass of the 3rd egg in the clutch (Fig. 3). The correlation between male hybrid index and mass of the 3rd egg was not significant, although it showed the same trend ($r = -0.276$, $df = 47$, $P = 0.055$). No significance was found in the correlation between female back-wingtip score and mass of the 3rd egg ($r = 0.008$, $df = 47$, $P = 0.955$), or between female hybrid index and the mass of the 3rd egg ($r = -0.090$, $df = 47$, $P = 0.537$). Ordinal logistic regression showed no significant correlation between hatching success or clutch size and hybrid index (Table 3) or adjusted hybrid index (Table 4).

DISCUSSION

Protection Island is located toward the northern boundary of the hybrid zone (Bell 1996), so as expected the phenotypes on the Violet Point gull colony tended toward *L. glaucescens*. The scarcity of *L. occidentalis*-type gulls on the colony was also noted by Bell (1996). After collecting 17 gulls from Protection Island, he determined that 8 were *L. glaucescens*, 8 were hybrids, and 1 was *L. occidentalis*. We found that females appeared significantly more like *L. occidentalis* than males

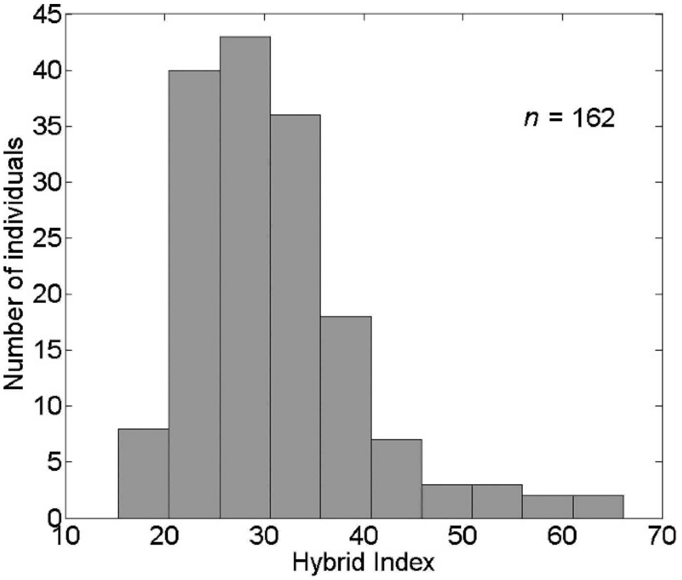

FIGURE 1. Distribution of hybrid indices for gulls on Violet Point, Protection Island. Mean = 30.7, median = 29.5. A lower hybrid index indicates a more *L. glaucescens*-like phenotype; a higher hybrid index indicates a more *L. occidentalis*-like phenotype.

in terms of wingtip, iris, and hybrid index scores. The reason for these differences is unknown, and we hesitate to assign them any biological significance.

We observed significant assortative mating by morphology across our sample of 81 gull pairs; however, it appears that *L. occidentalis*-like gulls mated more assortatively than *L. glaucescens*-like gulls. Whereas the more numerous *L. glaucescens*-like gulls showed little preference between mates in the 20 to 40 hybrid index range, the less numerous *L. occidentalis*-like individuals seemed to strongly prefer mates with a hybrid index >40 (Fig. 2). Hoffman and others (1978) and Bell (1997) also documented assortative mating based on colorimetric characters in gulls of the *L. glaucescens-occidentalis* complex. In contrast, Good and others (2000) found weak evidence of assortative mating on one colony and none on another colony. Although assortative mating is an indication of species divergence (Hoffman and others 1978), the absence of assortative mating does not necessarily indicate conspecificity, given that selection could preserve the parental species outside the hypothesized zone of hybrid superiority (Good and others 2000). Because we documented significant assortative mating, as did investigators in 2 of 3 previous studies, we believe that this mating pattern is regularly present among gulls in the hybrid zone. The evidence that hybrids are confined to the ecotone in coastal Washington and Oregon also suggests distinctness between the 2 parental species (Good and others 2000). In agreement with previous investigators, we believe that *L. glaucescens* and *L. occidentalis* should continue to be considered separate species due to the regular presence of assortative mating and the bounded nature of the hybrid zone (Hoffman and others 1978; Bell 1996; Good and others 2000). If the hybrid zone were to expand well beyond coastal Washington and Oregon in the coming years, this view should be carefully reconsidered.

TABLE 2. Summary of male and female character scores (mean and standard deviation) and Mann-Whitney *U* tests ($n = 81$ pairs).

	Male	Female	U	P
Back	4.79 (1.17)	5.00 (1.21)	2883	0.17
Wingtips	4.27 (1.59)	4.79 (1.85)	2634	0.03
Beak	4.89 (2.44)	4.48 (2.51)	3206	0.76
Orbital ring	2.44 (2.83)	2.17 (2.34)	3206	0.73
Iris	3.72 (2.73)	5.72 (2.84)	2120	0.00001
Hybrid index	29.17 (9.48)	32.25 (8.04)	2233	0.0004

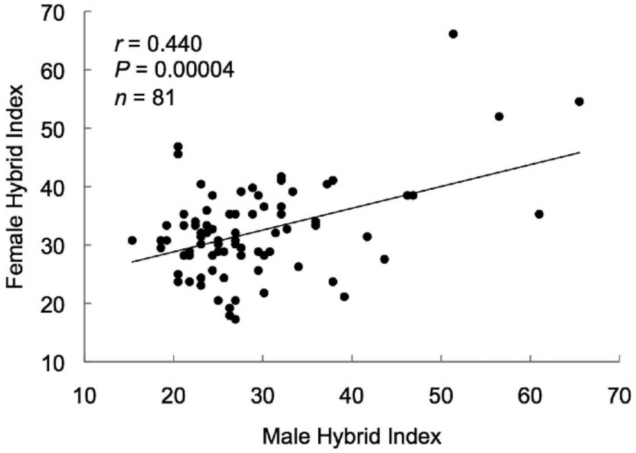

FIGURE 2. The correlation between male hybrid index and female hybrid index was significant, suggesting that assortative mating did occur.

The specific cues used by gulls to mate assortatively are debatable. Pierotti (1987) suggested that mate choice among seabirds is directed by similarity in the coloration of the beak and feet. This may be an important factor on Protection Island, as the most *L. occidentalis*-like individuals consistently showed an orange beak and bright pink legs, whereas intermediates and *L. glaucescens* typically showed yellower beaks and paler pink legs. It is difficult, however, to eliminate the possibility that plumage melanism, orbital ring color, or iris color add specificity to mate choice. Behavioral and auditory cues may influence mate choice as well, but more study is needed. A rather different explanation for the assortative mating observed among *L. occidentalis*-like individuals is that they were dispersers from colonies further south. Established members of the colony may recognize dispersers as less fit mates, leading dispersers to mate with each other (Hoffman and others 1978).

Most gulls produce 3-egg clutches (Good and others 2000), and the mass of the 3rd egg in the clutch appears to be a good indicator of diet quality and female energy reserves (Pierotti and Bellrose 1986; Bell 1997; Ramírez and others 2011). However, the significant negative correlation between male back-wingtip score and mass of the 3rd egg was unexpected. We are not

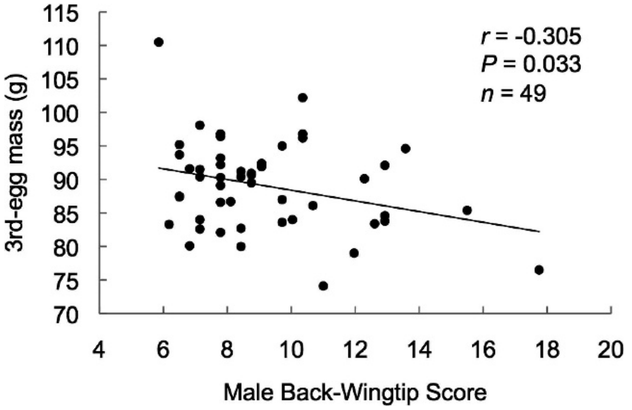

FIGURE 3. The negative correlation between male back-wingtip score and mass of the 3rd egg in the clutch was significant, meaning that the mass of the 3rd egg in the clutch decreased for increasingly *L. occidentalis*-like males.

TABLE 3. Coefficients (β) and their standard errors ($S_{\bar{x}}$), *P*-values, odds ratios (*OR*), and 95% confidence intervals for the *OR*s for ordinal logistic regression of clutch size and number of eggs hatched against male, female, and pair hybrid indices. *OR*s quantify the change in the odds of having a greater outcome (clutch size or hatching success) resulting from a change *c* in the independent variable (hybrid index). For clutch size analyses, $n = 81$. For hatching success analyses, $n = 69$. The hybrid index (HI) of each individual or pair is a number value that describes colorimetric phenotype. A lower HI indicates a more *L. glaucescens*-like phenotype; a higher HI indicates a more *L. occidentalis*-like phenotype.

	β	$S_{\bar{x}}$[a]	*P*	*c*	*OR*[b]	95% CI	
Clutch size							
Male HI	0.0292	0.03	0.25	10	1.34	0.81	2.21
Female HI	0.0107	0.03	0.70	10	1.11	0.65	1.92
Pair HI	0.0147	0.02	0.36	20	1.34	0.72	2.50
Eggs hatched							
Male HI	0.0259	0.02	0.26	10	1.30	0.83	2.03
Female HI	0.0003	0.03	0.99	10	1.00	0.60	1.68
Pair HI	0.0104	0.01	0.47	20	1.23	0.70	2.16

[a] Dispersion estimated.

[b] $OR > 1$ indicates that the odds of having a greater clutch size or hatching success increase as the hybrid index increases.

aware of any previous study that documented a significant decrease in egg mass with a more *L. occidentalis*-like phenotype. The absence of a similar trend with the female back-wingtip score is noteworthy, and it suggests that males have a role in determining egg mass. Because males are primarily responsible for supplying females with food during the pre-egg-laying period (Pierotti 1981), we infer that the ability of males to feed females is among the factors that influence egg mass.

Although the smaller 3rd-egg mass of pairs with more *L. occidentalis*-like males suggests poorer breeding success of these pairs (Krist 2011), we observed no significant difference between *L. glaucescens*-like and *L. occidentalis*-like gulls or between hybrid-like and parental-like gulls in terms of clutch size or hatching success, both of which are more direct measures of breeding success. In previous work, several investigators have suggested that the hybrid zone is maintained by the consistent ability of hybrids to outcompete parental species (Hoffman and others 1978; Good and others 2000). However, hybrids did not demonstrate this ability in our study. The borders of the hybrid zone presumably are formed where the parental species, *L. glaucescens* to the north and *L. occidentalis* to the south, begin to out-compete hybrids. Because Protection Island is located near the northern border of the hybrid zone, we were unsure how the breeding success of hybrids would compare to that of *L. glaucescens*. We hypothesized, however, that both hybrids and *L.*

TABLE 4. Coefficients (β) and their standard errors ($S_{\bar{x}}$), *P*-values, odds ratios (*OR*), and 95% confidence intervals for the *OR*s for ordinal logistic regression of clutch size and number of eggs hatched against male, female, and pair adjusted hybrid indices. *OR*s quantify the change in the odds of having a greater outcome (clutch size or hatching success) resulting from a change *c* in the independent variable (hybrid index). For clutch size analyses, $n = 81$. For hatching success analyses, $n = 69$. The adjusted hybrid index (AHI) of each individual or pair reflects the distance of its hybrid index from the midpoint of the observed range of hybrid indices. A lower AHI indicates a more hybrid-like phenotype; a higher AHI indicates a more parental-like phenotype.

	β	$S_{\bar{x}}$[a]	*P*	*c*	*OR*[b]	95% CI	
Clutch size							
Male AHI	−0.050	0.04	0.21	10	0.60	0.28	1.33
Female AHI	−0.003	0.04	0.94	10	0.97	0.47	2.01
Pair AHI	−0.022	0.02	0.35	20	0.64	0.25	1.64
Eggs hatched							
Male AHI	−0.030	0.04	0.44	10	0.74	0.35	1.57
Female AHI	0.043	0.04	0.24	10	1.54	0.75	3.14
Pair AHI	−0.004	0.02	0.87	20	0.93	0.38	2.28

[a] Dispersion estimated.

[b] $OR < 1$ indicates that the odds of having a greater clutch size or hatching success decreases as the adjusted hybrid index increases.

glaucescens would have greater breeding success than *L. occidentalis*, because *L. occidentalis* is at the northern reaches of its range on Protection Island. Our data suggest that neither *L. glaucescens* nor hybrids were more reproductively successful than *L. occidentalis*. Bell (1997) found that *L. occidentalis* pairs had the greatest breeding success among gulls in the hybrid zone, in contrast to the finding of Hoffman and others (1978) and Good and others (2000) that pairs containing hybrids were reproductively superior. He suggested that annual variation in marine and coastal environments could account for shifts in breeding success among phenotypes. We agree with Bell that differences in colorimetric phenotype alone are insufficient to accurately predict breeding success of gulls in the *L. glaucescens-occidentalis* hybrid zone. Environmental conditions as well as nest-site habitat and age of parents may correlate more strongly with breeding success in any given year.

We avoided arbitrary distinctions between pure and hybrid birds because a precise method for separating their colorimetric phenotypes in the field has not been delineated. The effects of wear on primary feathers, often quite pronounced by the time of the breeding season (Howell and Dunn 2007), are not mentioned in previous studies. We found, however, that a wingtip score may differ considerably depending on whether one looks at worn versus intact primaries. Also, when scoring plumage with a gray scale, it is not clear from previous studies whether scores were based on the average shades or the darkest pigment visible. Although we scored plumage based on average feather shade in this study, we propose that in future work plumage scores should be based on the darkest feathers visible because melanin is associated with higher levels of keratin, a protein that strengthens feathers and reduces feather wear (Gill 1990; Sibley 2000). Such details in methodology must be standardized for studies of this type to be meaningfully compared.

Our work provides the first large scale description of colorimetric variability in gulls of the *L. glaucescens-occidentalis* complex on Protection Island, and the first comparison between colorimetric phenotype and breeding success of these gulls in the Salish Sea. We believe that our finding of significant assortative mating on Protection Island, although the trend appears to be due to a few *L. occidentalis*-like pairs, supports the current classification of *L. glaucescens* and *L. occidentalis* as separate species. The lack of differential breeding success among colorimetric phenotypes indicates that variables other than the appearance of the gulls were more strongly related to the breeding success of gulls in the *L. glaucescens-occidentalis* complex on Protection Island in 2010.

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