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Equal reproductive success of phenotypes in the *Larus glaucescens–occidentalis* complex

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Glaucous-winged gulls *Larus glaucescens* and western gulls *L. occidentalis* hybridize extensively where their ranges overlap along the coasts of Washington and Oregon, producing a continuum of phenotypic intergrades between the two parental species. This zone often is considered an example of geographically bounded hybrid superiority, but studies of relative success among parental types and hybrids have not provided consistent support for this model. We tested the predictions of the dynamic-equilibrium and geographically bounded hybrid superiority hypotheses by studying mate choice and reproductive success among gulls on Protection Island, Washington, the largest breeding colony of glaucous-winged/western gulls within the hybrid zone. The dynamic-equilibrium hypothesis posits that hybridization due to dispersal balances selection against less fit hybrids and assortative mating is adaptive. Geographically bounded hybrid superiority posits that hybrids are better fit than parental types within an ecotone between the environments to which the parental species are adapted, and a preference for hybrid mates is adaptive. Additionally, we investigated whether hatching success and nest site choice are correlated for Protection Island gulls. We assigned a hybrid index to each sample bird by examining plumage melanism and bare part coloration in the field. Sheltered nests contained larger clutches and exhibited increased hatching success, but choice of nest habitat was not associated with hybrid index. Western gull-like pairs produced smaller third eggs; however, hybrid index was not correlated with clutch size or hatching success. Protection Island gulls did exhibit assortative mating. In short, we did not find strong support for either geographically bounded hybrid superiority or the dynamic-equilibrium hypothesis.

The *Larus glaucescens–occidentalis* hybrid zone in the Pacific Northwest has been the subject of several studies since hybrids were first noted early in the twentieth century (Dawson 1908). These species hybridize extensively along the coasts of Washington and northern Oregon where their breeding ranges overlap, and the hybrids exhibit a continuum of phenotypic intergrades (Hoffman et al. 1978, Bell 1996, 1997). Although it is the best-studied gull hybrid zone and often cited as one of the best avian examples of geographically bounded hybrid superiority (Price 2008), studies have not clearly supported this model.

Two main models have been applied to the *L. glaucescens–occidentalis* hybrid zone: 1) the dynamic-equilibrium, or tension zone, hypothesis in which hybridization due to dispersal balances selection against less fit hybrids and assortative mating is adaptive (Hewitt 1988, Gay et al. 2008); and 2) the geographically bounded hybrid superiority hypothesis, in which hybrids are better fit than parental types within an ecotone between the environments to which the parental species are adapted, and a preference for hybrid mates is adaptive (Moore 1977, Good et al. 2000). Support has been found for each model and it is unclear which most accurately describes the dynamics of the *L. glaucescens–occidentalis* zone. Our understanding of the fitness characteristics of phenotypes in this zone remains limited, although patterns of relative success best differentiate between the two hypotheses.

The *L. glaucescens–occidentalis* zone typically is considered a narrow zone (Barton and Hewitt 1985, Bell 1996), although the zone has expanded (Hoffman et al. 1978, Bell 1996, Good et al. 2000) since hybrids first were noted by Dawson (1908, 1909). Moreover, genetic evidence suggests the zone has shifted south (Gay et al. 2008). However, concordance and narrowness of morphological and genetic clines indicate that the two species are not fusing; that is, the hypothesis of neutral diffusion is rejected (Gay et al. 2008).

Here we test the predictions of the dynamic-equilibrium and geographically bounded hybrid superiority hypotheses by studying mate choice and reproductive success in the largest breeding colony of glaucous-winged/western gulls within the hybrid zone (Larsen 1982, Speich and Wahl 1989). For purposes of our analysis we accept as a first assumption that this zone is stable, or at least persistent, because fitness predictions are not clear for a moving tension zone. We then test the following specific predictions (Fig. 1): 1) hybrids exhibit reduced reproductive success compared to parental types and gulls mate assortatively (dynamic-equilibrium

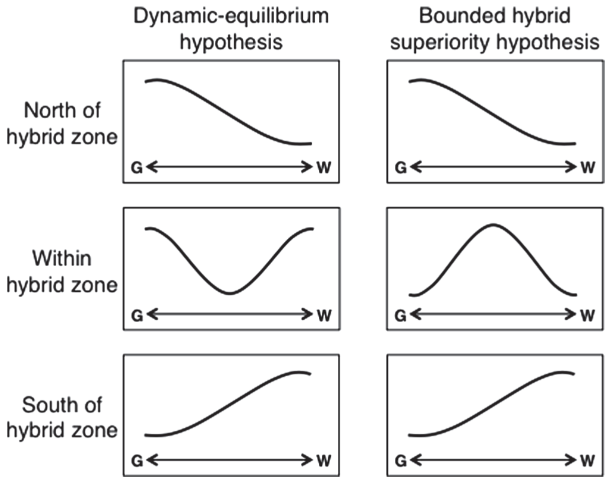

Figure. 1. Predictions of relative fitness by two hybrid zone models for populations north of the zone, within the zone, and south of the zone. The horizontal axis within each box represents the hybrid index, placing phenotypes from glaucous-winged gull-like (G) to western gull-like (W). Predictions of relative fitness are indicated by the curves.

hypothesis); 2) hybrids exhibit greater success than parental types and assortative mating is weak or nonexistent (geographically bounded hybrid superiority hypothesis; colony lies within area of hybrid superiority); 3) glaucous-winged gulls exhibit greater success than both hybrids and western gulls and gulls may or may not mate assortatively (dynamic-equilibrium hypothesis, or geographically bounded hybrid superiority hypothesis where the colony lies north of the area of hybrid superiority).

We also investigate whether pairs with dissimilar mates suffer decreased success and whether nest site choice drives differential success among parental types and hybrids.

Methods

Study site and nest monitoring

Our study was carried out at Protection Island National Wildlife Refuge (48°07′40″N, 122°55′40″W), Jefferson County, Washington, at the southeastern border of the Strait of Juan de Fuca. Violet Point, a low-lying gravel spit, extends 0.8 km from the eastern side of the island and typically hosts 2500–3000 breeding pairs of gulls (Cowles et al. 2012).

From 27 May through 15 July 2011, we monitored gull nests daily adjacent to and west of the marina. At clutch initiation we marked each nest with a numbered wooden stake. We labeled each new egg with a letter according to its order of appearance within the nest. We weighed each new egg to the nearest 0.1 g using an Ohaus Scout Pro SP401 portable scale. Mass of the third, and commonly last, egg of a clutch is used as a measure of success because size of the third egg is dependent on the energy reserves of the female. If food is abundant, the third egg can be as large as the first two eggs of the clutch (Pierotti and Bellrose 1986). Fourth, fifth, and sixth eggs accounted for 1% of the data and were not included in analyses of egg mass. Every day we noted whether each egg still was present or if it was hatched, addled, pipping, missing, or dead for some other reason. We defined hatching success as the number of chicks hatched successfully from the nest regardless of the clutch size. We defined successful nests as those that hatched at least one egg and unsuccessful nests as those that hatched no eggs.

We designated each nest site as 'sheltered' or 'unsheltered'. Sheltered nests were located next to logs taller than the nest rims, next to the eroded bank around the marina, or beside vegetation taller than the nests. Unsheltered nests were typically in short or sparse vegetation or on beach/marina cobblestones.

We could not obtain hatching success data for all nests: monitoring became too risky when chicks were several days old, mobile, and thus vulnerable to cannibalism. Unfinished nests were followed long enough for us to be certain of clutch size; hence, analyses of clutch size included finished and unfinished nests. Analyses of hatching success included only finished nests.

Assignment of hybrid indices

Two observers (LCM and AEM) viewed gulls 3–5 m distant through a Nikon Fieldscope ED82 and classified them within the *L. glaucescens–occidentalis* spectrum using a hybrid index patterned after that of Bell (1997) and Good et al. (2000, Howell and Dunn 2007). The index consisted of scores for back (mantle plus scapulars) shade, shade of primary tips, bill color, orbital ring color, and iris color. We scored plumage characters according to a Kodak 20-step neutral gray scale (CAT 152 7654) and bare part colors according to a 1–5 scale similar to that of Bell (1997) and Good et al. (2000); Supplementary material Table A1–1. We independently scored each character; scores were averaged if after discussion we did not agree. We termed these original Kodak and bare part scores 'raw scores'. We obtained scores from 15 June through 14 July 2011 when cloud cover rendered lighting conditions relatively consistent and good for observation of gray shades (Howell and Dunn 2007). We began data collection no earlier than 08:00 PDT and terminated it when the sunlight became bright enough to cause shadows (solar flux ≈ 300 W m^{-2}). Sunny conditions washed out differences in shades.

Scores were obtained for all characters of 169 pairs and an additional 16 males and 40 females, a total of 394 birds. Analyses of hybrid indices alone were carried out on this dataset. We obtained complete hybrid indices and nesting data (egg masses, clutch size, hatching success) for 147 pairs and an additional 13 males and 29 females.

Analysis

We converted the raw scores into 'character scores' by rescaling the observed range of the raw scores equally from 1–10 (Supplementary material Table A1–1). We created a weighted index by adding the scaled (1–10) bare part scores to twice the sum of the scaled plumage scores:

$$\begin{aligned}\text{Hybrid index} = {} & 2\ (\text{back}) + 2\ (\text{wingtips}) \\ & + \text{beak} + \text{orbital ring} + \text{iris}\end{aligned}$$

All analyses used these weighted hybrid indices. We refer to the weighted hybrid index for the male of a pair as the 'male index' and the weighted hybrid index for the female of a pair as the 'female index'. Male and female indices were summed to produce the 'pair index'. A higher index score indicates an individual more like a pure western gull.

Logistic regression detects only linear trends in the outcome with respect to the independent variable; thus, analysis of hybrid index alone will likely not detect cases where hybrids have increased or decreased success relative to parental types. To determine if such was the case, we calculated the 'index distance to midpoint' (IDM) for each male, female, and pair index. For male and female hybrid indices, the IDM is the absolute value of the difference between the index and the midpoint of the possible range of indices. The hybrid index for individual birds can range from 7–70, thus:

$$\text{IDM} = | \text{index} - 38.5 |$$

For pair indices, the IDM was calculated by:

$$\text{Pair IDM} = | \text{pair index} - 2(38.5) |$$

Higher values of IDM represent individuals that are more like pure glaucous-winged or western gulls, while lower values represent 'hybrids' or intermediate birds. This transform linearizes the relationship between outcome and independent variable in the event that intermediate types have different success than parental types. The midpoint may not be representative of a 'typical' hybrid, but we use it as a reasonable approximation.

To determine if pre- or post-zygotic incompatibilities between dissimilar mates affected reproductive success, we calculated the 'pair difference' for each pair:

$$\text{Pair difference} = |\text{male index} - \text{female index}|$$

Larger values of the pair difference indicate more dissimilar mates.

We used MATLAB with Statistics Toolbox to conduct ordinal logistic regression and all statistical tests except the Mann–Whitney U test, which we performed in SPSS. We based our decision to use a parametric or nonparametric test for each analysis on histograms and normal probability plots of the data. All tests were carried out at the $\alpha = 0.05$ significance level.

We used proportional odds model ordinal logistic regression (mnrfit in MATLAB) to test whether hatching success or nest success was correlated with hybrid index or IDM or pair difference, clutch size, and an interaction term between clutch size and hybrid index or IDM (see Catry et al. 1999 for an example of ordinal logistic regression used in a similar context). Ordinal logistic regression assumes a linear relationship between the independent variable and the transformed response variable. Thus, ordinal logistic regression of success outcomes on hybrid indices allowed us to determine whether either parental type had significantly different success than the other, whereas the ordinal logistic regression of success outcomes on IDMs allowed us to determine whether intermediate types had significantly different success than parental types. Regression of hatching success (or nest success) on the interaction term allowed us to determine whether hybrid index or IDM were correlated with hatching success (or nest success) for a given clutch size.

Results

Colony composition and assortative mating

Our sample of 394 birds contained 8% of the colony's approximately 4800 breeding gulls (J. Galusha pers. comm.). Putatively pure individuals of both glaucous-winged gulls and western gulls occurred on the colony, but glaucous-winged gulls and/or glaucous-winged gull-like hybrids dominated the colony. Relatively few individuals exhibited the very pale wingtips of 'classic' glaucous-winged gulls (Fig. 2).

The hybrid indices of paired males and females were significantly positively correlated (Pearson's $r = 0.35$, $p = 0.000003$; Fig. 3). Individual character scores of males and females in pairs were significantly positively correlated (Pearson's correlation, all $r > 0.27$, all $p \leq 0.0005$, except for iris scores (Pearson's correlation, $r = 0.11$, $p = 0.16$).

Nest site choice and reproductive success

Male, female, and pair indices were not significantly different for sheltered and unsheltered nests (two-tailed Mann–Whitney U, all $p > 0.44$). Male, female, and pair IDMs also were not significantly different for sheltered and unsheltered nests (two-tailed Mann–Whitney U, all $p > 0.06$). First, second, and third egg masses were not significantly different across nest site types (two-tailed independent t-test, all $p > 0.22$). Clutch size and hatching success were significantly different across nest site types, with sheltered nests having larger clutch sizes and greater hatching success (two-tailed Mann–Whitney U; $p = 0.014$ and $p < 0.001$, respectively). The main driver of decreased success for unsheltered nests was egg cannibalism: 14% of eggs in sheltered nests were cannibalized, whereas 27% of eggs in unsheltered nests were cannibalized.

First and second egg masses were not significantly correlated with male index, female index, or pair index (Pearson's correlation, all $p > 0.71$); third egg mass was not correlated with male or female index (both $p > 0.11$). However, third egg mass was significantly negatively correlated with pair

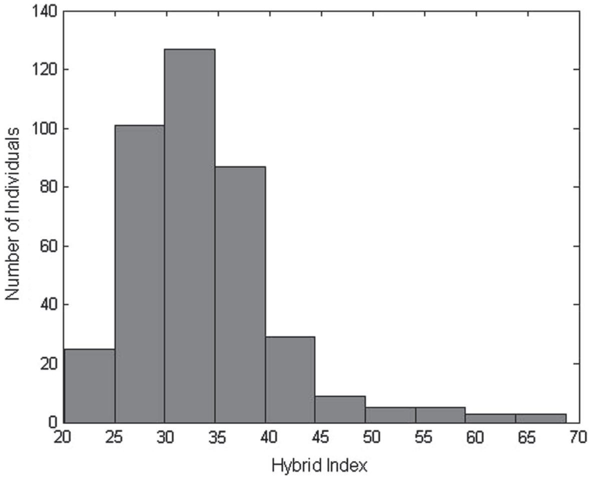

Figure 2. Frequency distribution of hybrid indices for all individuals observed ($n = 394$). Higher values of the index represent more western gull-like individuals.

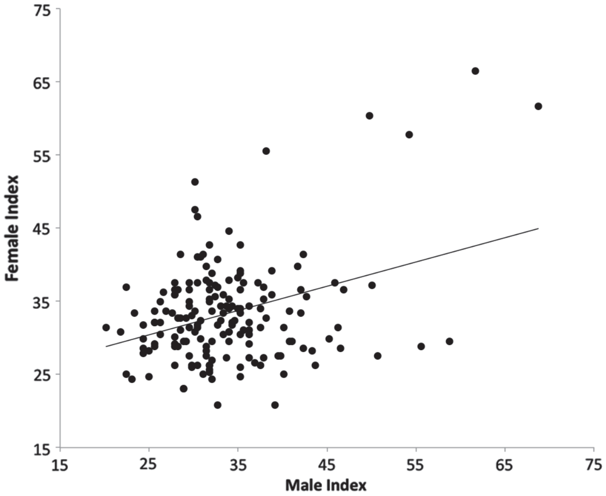

Figure 3. Correlation of hybrid indices between males and females of pairs (n = 169). This relationship is significant (r = 0.35, $p < 0.0001$). Higher values of the index represent more western gull-like individuals. Linear trend line for all data is shown.

index (r = –0.178, p = 0.041). Thus, third eggs of western gull-like individuals tended to be smaller than third eggs of glaucous-winged gull-like individuals. First, second, and third egg masses were not significantly correlated with IDM (Pearson's correlation, all $p > 0.17$).

Hatching success was not significantly correlated with pair difference, male, female, or pair hybrid index, nor was it correlated with male, female, or pair IDM (ordinal logistic regression, all $p > 0.13$, Supplementary material Table A2–1). Hatching success was positively correlated with clutch size in two of these seven analyses (ordinal logistic regression, both $p < 0.05$, Supplementary material Table A2–1). Hatching success was not correlated with the interaction term in any of the analyses (ordinal logistic regression, all $p > 0.08$, Supplementary material Table A2–1). Nest success was significantly correlated with male index and pair IDM only (ordinal logistic regression, both $p < 0.05$, Supplementary material Table A2–2); nest success was also correlated with the interaction term in those analyses (both $p < 0.05$). Nest success was correlated with clutch size in one of these seven cases (ordinal logistic regression, p = 0.01, Supplementary material Table A2–2).

Discussion

We found that gulls on Protection Island mated assortatively but that all phenotypes experienced equal hatching success. Because we obtained significance for only two analyses of nest success and phenotype we conclude that phenotype has no strong effect on nest success at this colony. Furthermore, dissimilar pairs did not experience decreased success; and although clutch size and hatching success were greater for sheltered nests no phenotype was more likely to choose sheltered nest sites.

Methodology

Hybrid indices of Protection Island gulls spanned a continuous range (Fig. 2). Because *L. glaucescens*, *L. occidentalis* and *L. glaucescens–occidentalis* hybrids have not been defined in terms of Kodak scores, we chose analytic methods that did not require us to split the hybrid index into artificial categories. Thus, instead of referring to individuals as 'glaucous-winged gulls' we refer to individuals as 'glaucous-winged gull-like' if their indices placed them towards the low end of our hybrid index; these individuals may in fact be either pure *L. glaucescens* or hybrids. This tactic gave us an accurate depiction of relative success among phenotypes without relying on assumptions about what is a pure or hybrid bird.

Assortative mating

Mating patterns aid determination of the appropriate model: if hybrids have greater reproductive success, birds that choose hybrid mates are more successful; if hybrids are less successful, assortative mating is advantageous. Both Hoffman et al. (1978) and Bell (1997) found a strong tendency for individuals to pair with mates having a similar phenotype but Good et al. (2000) found weak or no correlations between hybrid indices of males and females.

With Hoffman et al. (1978) and Bell (1997), we found a strong tendency for individuals to pair with mates exhibiting a similar phenotype. Western gull-like individuals paired with mates that also were western gull-like. Individuals with intermediate and glaucous-winged gull-like hybrid indices, however, did not necessarily pair with individuals exhibiting a similar hybrid index, although they typically paired with other intermediate or glaucous-winged gull-like individuals. It may be that individuals at the extreme ends of the hybrid index tend to mate assortatively whereas more intermediate individuals will accept a wider phenotypic range of mates; or possibly this result is an artifact due to our small sample of very western gull-like birds.

Nest site choice and reproductive success

Movement of the hybrid zone supports the dynamic-equilibrium hypothesis because a tension zone is mobile until dispersal of parental types comes to equilibrium with selection against hybrids; the zone is not anchored by fitness differences due to (for instance) an ecotone (Barton and Hewitt 1985, Hewitt 1988, Gay et al. 2008). Two studies of reproductive success, however, supported the geographically bounded hybrid superiority hypothesis. Hybrid pairs on Destruction Island, Washington, hatched chicks more successfully than did pure glaucous-winged or western gull pairs (Hoffman et al. 1978). Good et al. (2000) demonstrated that pairs that included hybrid individuals had greater clutch size, egg volume, hatching success, and fledging success. Greater success of hybrids was ascribed to their ability to combine adaptive behaviors of both parent species. Hybrids in Grays Harbor, Washington had significantly greater reproductive success than western gulls because they chose nest sites sheltered by vegetation, which reduced predation of eggs. Hybrids on Tatoosh Island, Washington had significantly greater hatching and fledging success than glaucous-winged gulls because the hybrids fed predominantly on fish rather than intertidal invertebrates.

Reported egg masses for western and glaucous-winged gulls broadly overlap (Pierotti and Bellrose 1986, Verbeek 1986, Pierotti and Annett 1995, Hayward and Verbeek 2008) and egg masses for Protection Island gulls are consistent with reported data for both species (93.6 ± 7.69 g, n = 2932; Hayward et al. 2014). Thus, we assume that trends in our data are due to female condition rather than species differences. Western gull-like individuals on Protection Island tended to have smaller third eggs and thus by this indicator were less successful than hybrids and glaucous-winged gulls. Egg mass is a relatively indirect measure of fitness, however, and western gulls were not less successful according to the more direct measures of hatching success and nest success. Additionally, pairs composed of more dissimilar mates did not experience decreased success compared to pairs of similar birds. Analysis of regurgitated boli (Lindborg et al. 2012) suggests that landfill waste plays a minor role in the diet of Protection Island gulls; thus, we assume that access to artificial food sources is not affecting relative reproductive success.

Sheltered nests contained larger clutch sizes and exhibited better hatching success than unsheltered nests. Because hybrid indices and IDMs are not different for the two site types, however, there is no evidence that any particular phenotype selects one habitat over the other. In Grays Harbor, Washington, hybrids were more successful than western gulls because they chose nest sites sheltered by vegetation (Good et al. 2000, Good 2002). In contrast, western gull-like individuals on Protection Island did not usually choose unsheltered nest sites: seven of 10 pairs with the greatest hybrid indices chose sheltered nest sites.

A modification of the geographically bounded hybrid superiority hypothesis has been suggested: selection–hybridization balance, in which hybrids are favored only during some breeding seasons due to annual environmental fluctuations (Grant and Grant 1992, Bell 1997). We are unable to rigorously test this hypothesis because our study

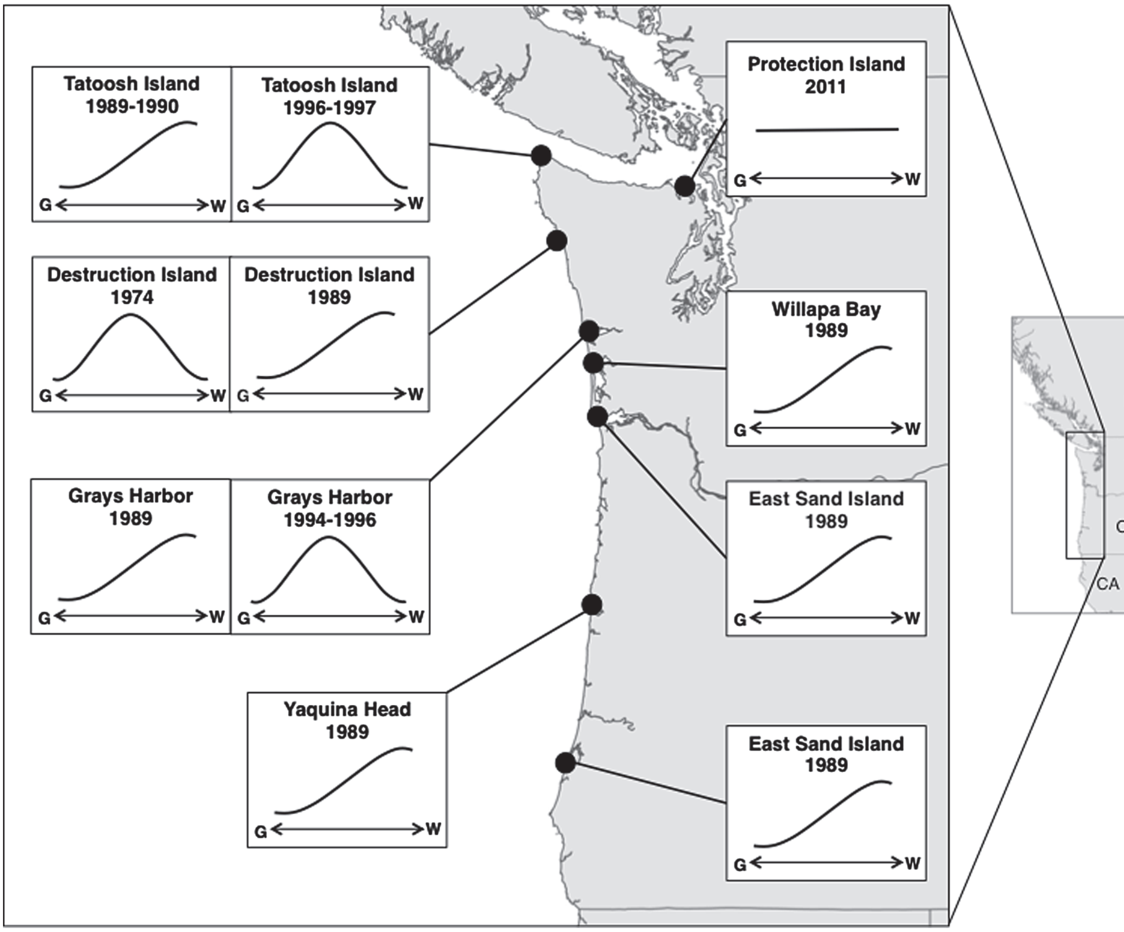

Figure 4. Schematic summary of relative fitness results from studies in the *Larus glaucescens–occidentalis* hybrid zone. The horizontal axis represents the hybrid index, placing phenotypes from glaucous-winged gull-like (G) to western gull-like (W). Relative fitness results are indicated by the curves. The 1974 Destruction Island study was conducted by Hoffman et al. (1978), who determined that hybrids experienced greatest hatching success. The 1989 and 1990 studies were conducted by Bell (1997), who determined that western gulls had the smallest egg volume differences (largest relative C egg volume) at eight sites (two in Grays Harbor) in Washington and Oregon. The studies on Tatoosh Island and in Grays Harbor were conducted by Good et al. (2000), who determined that hybrids experienced greatest hatching and fledging success. Note that our schematic slightly misrepresents the findings of Good et al. (2000), who did not claim to have found pure western gulls on Tatoosh or pure glaucous-winged gulls in Grays Harbor. Map: Esri, DeLorme Publishing Company. Used with permission.

was conducted over only one season. Equal relative success of all phenotypes, however, does not match fitness predictions of the selection–hybridization hypothesis: either hybrids or a parental species has greatest fitness in a given year. Limited data from a 2010 study (Moncrieff et al. 2013) on Protection Island also showed no significant relationship between hybrid index and clutch size or hatching success.

Limitations

Likely our sample of gulls was not truly random. Although we tried to obtain character scores for all birds within our study plots, we were not entirely successful: wary birds flew at our approach. Furthermore, birds in different sub-regions of the colony experience different pressures, e.g. amount of eagle predation (Hayward et al. 2010) or egg cannibalism (Hayward et al. 2014), and have differential hatching success (Hayward et al. 2014). We did not collect character scores until most birds were well into egg-laying or beginning incubation so early nesters that abandoned before our study began were not included. Thus, our sample may have been biased towards more successful gulls and did not capture the entire range of success outcomes experienced by the birds.

We were unable to follow chicks to fledging and thus cannot comment on whether the gulls might experience differential fledging success. Good et al. (2000), however, found that when hybrids experienced greater hatching success, they also experienced greater fledging success. Nests sheltered by vegetation produce more fledglings (Good 2002); but because we found no strong correlation between hybrid index and nest habitat choice, comparing chick survival across nest site types may not be informative.

Conclusions

Reproductive success was not significantly greater for intermediate phenotypes or for pure glaucous-winged or western individuals, although gulls did mate assortatively. We found no evidence of differential nest habitat choice according to phenotype.

Thus: 1) we reject the dynamic-equilibrium hypothesis; hybrids did not exhibit decreased success compared to parental types. However, this rejection is tentative because we did find evidence of assortative mating; 2) we reject the geographically bounded hybrid superiority hypothesis for a colony that lies within the area of hybrid superiority; hybrids were not most successful and the gulls mated assortatively; 3) we reject both the dynamic-equilibrium and geographically bounded hybrid superiority hypotheses for a colony that lies north of the zone; glaucous-winged gulls were not most successful.

It is possible that Protection Island is on or near the boundary between hybrid superiority and glaucous-winged gull superiority, and thus these phenotypes are equally successful. This explanation fails to account, however, for equal success among western gull-like individuals as well.

Evidence to date regarding relative fitness of hybrids and parental types within the zone is summarized in Fig. 4. Equal reproductive success across phenotypes suggests fusion following secondary contact: extensive introgression unchecked by fitness consequences should ultimately meld the two species. Expansion of the zone over the past century also is consistent with this scenario. Conversely, the persistence of the zone and evidence of assortative mating imply relative fitness differences across the range of phenotypes, findings contrary to predictions of the neutral diffusion model.

Equal reproductive success has been noted for another hybrid zone to which the geographically bounded hybrid superiority hypothesis has been widely applied: the northern flicker zone, where subspecies *Colaptes auratus auratus* and *C. a. cafer* hybridize. Hybrids at the northern end of the hybrid zone had no advantage in agonistic contests, hatching success, or fledging success; long-term survival was determined by large-scale weather patterns rather than phenotype (Flockhart and Wiebe 2009).

The results of our study and ambiguity in the combined results of earlier studies suggest it is still premature to provide a causal explanation for the existence of the *Larus glaucescens–occidentalis* hybrid zone.

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Supplementary material (Appendix JAV-00421 at <http://www.avianbiology.org/readers/appendix>). Appendix A1–A2.