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ABSTRACT

REPRODUCTIVE SUCCESS OF GULLS IN THE *LARUS GLAUCESCENS*-
OCCIDENTALIS COMPLEX ON PROTECTION
ISLAND, WASHINGTON

by

Libby C. Megna

Co-Chairs: James L. Hayward
Shandelle M. Henson

ABSTRACT OF GRADUATE STUDENT RESEARCH

Thesis

Andrews University

College of Arts and Sciences

Title: REPRODUCTIVE SUCCESS OF GULLS IN THE *LARUS GLAUCESCENS- OCCIDENTALIS* COMPLEX ON PROTECTION ISLAND, WASHINGTON

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Date completed: April 2012

Glaucous-winged Gulls (*Larus glaucescens*) and Western Gulls (*Larus occidentalis*) hybridize extensively where their ranges meet along the coasts of Washington and Oregon, producing a continuum of phenotypic intergrades between the two parental species. Previous work has shown that hybrids can experience greater reproductive success than parental types by combining adaptive behaviors, such as nest site selection, of both parental species, although success of hybrids may be affected by shifts in the ecotone between marine upwelling and non-upwelling environments. I investigated whether there is a correlation between phenotype, reproductive success, and nest site choice for gulls in Protection Island National Wildlife Refuge, Washington. I examined plumage melanism and bare part coloration in the field to determine a hybrid index for each bird sampled; indices for each member of a sample pair were summed to

produce a pair index. Nests were monitored until eggs hatched; nest habitat was recorded as sheltered or unsheltered. Sheltered nests contained larger clutches and exhibited better hatching success but choice of nest habitat was not associated with hybrid index. Pair index was correlated with mass of the third egg of the clutch, with more Western Gull-like pairs producing smaller eggs. However, hybrid index was not significantly correlated with clutch size or hatching success. The distance of an index to the mode of the distribution of indices also was not correlated significantly with clutch size or hatching success; that is, the most abundant phenotypes on the colony were not significantly more or less successful than any other phenotypes.

Keywords: habitat choice, hybridization, *Larus glaucescens*, *Larus occidentalis*, hatching success

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OCCIDENTALIS COMPLEX ON PROTECTION
ISLAND, WASHINGTON

A Thesis
Presented in Partial Fulfillment
of the Requirements for the Degree
Master of Science

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For my parents

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CHAPTER 1

INTRODUCTION

Glaucous-winged Gulls (*Larus glaucescens*) breed along the outer coast from northern Oregon to southwest Alaska and the Aleutians and within the Salish Sea; their nonbreeding range includes the breeding range and extends south along the Baja California Peninsula (Sibley 2000; Howell and Dunn 2007). Western Gulls (*Larus occidentalis*) breed along the outer coast of Washington south to Baja California Sur; their nonbreeding range extends north to the Washington portion of the Salish Sea and south to the tip of the Baja California Peninsula (Sibley 2000; Howell and Dunn 2007). These two species hybridize extensively where their breeding ranges overlap along the coasts of Washington and northern Oregon (specifically, *L. glaucescens* hybridizes with *L. o. occidentalis*); this region is also an ecotone between marine upwelling and non-upwelling, fjord environments (Hoffman et al. 1978; Bell 1996, 1997; Sibley 2000; Wahl 2005).

Currently there is no precise definition of what constitutes a pure Glaucous-winged or Western Gull. Glaucous-winged Gulls are described as having pale gray backs and pale gray wingtips, pale yellow to bright yellow beaks, pink orbital rings, and typically dark irises, although the irises can be very pale (Bell 1997; Howell and Dunn 2007). A “classic” Glaucous-winged Gull has wingtips of approximately the same shade as the back (Sibley 2000); however, birds with wingtips some shades darker than the

back also are considered to be pure Glaucous-winged Gulls (Howell and Dunn 2007). Western Gulls have slaty gray backs and black wingtips—although individuals that have blackish or dark gray wingtips also are considered to be pure Western Gulls—bright yellow to orange beaks, yellow or yellow-orange orbital rings, and pale irises (Bell 1997; Howell and Dunn 2007).

Bell (1996) collected gulls from 33 colonies along the coasts of British Columbia, Washington, and Oregon to determine whether hybrids could be identified by their intermediate coloration. Canonical discriminant function analysis of colorimetric characters, calibrated with presumably pure birds collected from sites far from the hybrid zone and hybrids from within the hybrid zone, allowed classification of individuals as Glaucous-winged, Western, or hybrid. Indeed, hybrids possessed colorimetric characters intermediate between those of parental types, although Bell also demonstrated (via analysis of 25 enzyme systems) that hybrids are genetically more similar to Glaucous-winged Gulls.

Three main models have been applied to the *Larus glaucescens-occidentalis* hybrid zone: (1) the dynamic-equilibrium hypothesis, in which hybridization due to dispersal balances selection against less fit hybrids, and assortative mating is adaptive (Hewitt 1988; Gay et al. 2008); (2) geographically bounded hybrid superiority, where hybrids are more 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); and (3) selection-hybridization balance, where hybrids are favored only during some breeding seasons due to changes in the environment (Grant and Grant 1992; Bell 1997). The predictions of these models regarding relative fitness are

summarized in Figure 1. Some support has been found for each of these models; it is not yet clear which model most accurately describes the *L. glaucescens-occidentalis* hybrid zone.

Two studies have shown that hybrid individuals experience greater reproductive success within the hybrid zone. Hoffman et al. (1978) found that hybrid pairs on Destruction Island, Washington, in 1974 were more successful at hatching chicks than pure Glaucous-winged or Western pairs. Good et al. (2000) examined the breeding behavior of gulls at two colonies within the hybrid zone: one to the north (Tatoosh Island, WA), consisting of Glaucous-winged Gulls and hybrids, and one to the south (Grays Harbor, WA), consisting of Western Gulls and hybrids. Pairs that included one or two hybrid individuals experienced greater reproductive success as measured by clutch size, egg volume, hatching success, and fledging success. Good et al. (2000) ascribed the greater success of hybrids to their ability to combine adaptive behaviors of both parent species. Hybrids in the colony of mostly Western Gulls had significantly greater reproductive success due to their choice of nest sites sheltered by vegetation, which reduced predation of eggs. Hybrids in the colony of mostly Glaucous-winged Gulls had significantly greater hatching and fledging success; Good et al. (2000) postulated that the difference in success occurred because hybrids fed predominantly on fish rather than intertidal invertebrates, as did Glaucous-winged Gulls. Good et al. advanced the hypothesis that the model of geographically bounded hybrid superiority (see Moore 1977) best describes the *L. glaucescens-occidentalis* hybrid zone.

It should be noted, however, that the results of previous work do not all concur; it is not yet clear how far (both metaphorically and geographically speaking) results from

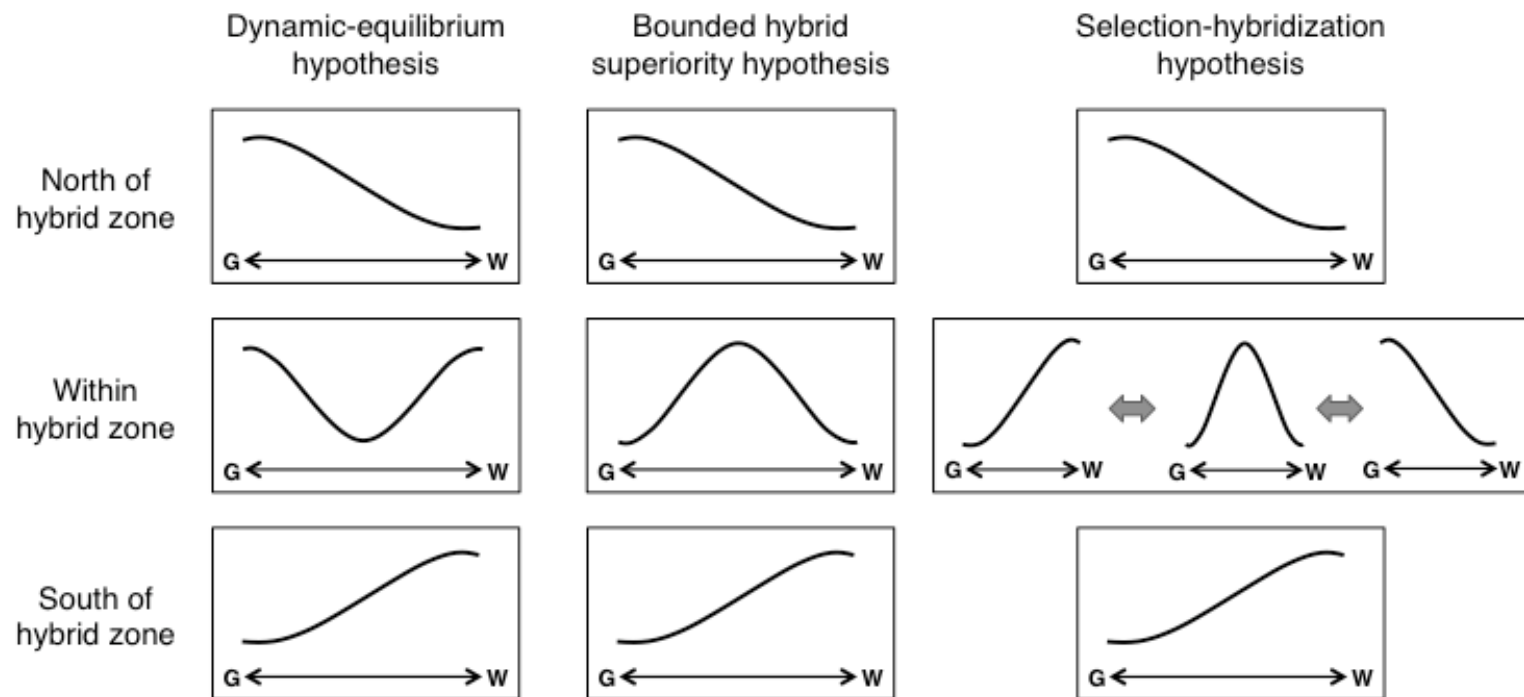
one colony may be extrapolated to others. Bell (1997) found that Western Gulls had larger egg volume and clutch sizes than both hybrids and Glaucous-winged Gulls at eight study sites along the coasts of Washington and Oregon, including Destruction Island, Washington. The reasons for this shift to greater Western Gull reproductive success are unknown; Bell postulated that the inconsistent results were due to a change in the width of the ecotone between marine upwelling and non-upwelling environments. Western Gulls presumably are adapted best to marine upwelling environments and so would be favored during years when upwelling is predominant within the hybrid zone; hybrids would be favored other years. Bell proposed that this selection-hybridization balance, where greatest relative fitness of pure birds and hybrids changes in time, maintains the *L. glaucescens-occidentalis* hybrid zone.

Evidence regarding the existence of assortative mating in this gull complex is also somewhat ambiguous: although both Hoffman et al. (1978) and Bell (1997) found a strong tendency for individuals to pair with mates having a similar phenotype (p-values < 0.001), Good et al. (2000) found only weak correlations between hybrid indices of males and females at one colony ($0.05 < p < 0.10$) and no correlation at another ($p > 0.10$). Classifying *L. glaucescens* and *L. occidentalis* as separate species has been based in part on the existence of assortative mating (Hoffman et al. 1978), and understanding mate choice is necessary to understand hybridization events in birds (Good et al. 2000).

This study was conducted on Protection Island in Washington, located in the Strait of Juan de Fuca. The island hosts what is believed to be the largest breeding colony of Glaucous-winged/Western Gulls in Washington (Larsen 1982), hosting 30% of the Washington breeding population (Speich and Wahl 1989), and has been the site of

numerous studies of “Glaucous-winged Gull” behavior and ecology (see Henson and Hayward 2010). Describing these birds in terms of the *Larus glaucescens-occidentalis* spectrum will be valuable for future work. Previous studies of reproductive success in this hybrid complex have been limited to outer coastal islands; it is not yet known whether hybrids also fare better in the Salish Sea and, if so, by what mechanisms they experience increased reproductive success. If hybrid superiority is bounded, it is not known exactly where the boundary lies geographically, or what factors (e.g., habitat choice) are most important in increasing hybrid success across the zone. This study adds another data point to the investigation of hybrid success across geographic space. This study also provides recent information about the degree of hybridization of Protection Island gulls, which can be compared to the data obtained by Bell (1996) in the 1980s. Finally, I test the hypothesis that the most abundant phenotype on the colony experiences the greatest egg production and/or hatching success.

Fig. 1. Predictions of relative fitness by three hybrid zone models. The horizontal axis 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. For the selection-hybridization hypothesis, the double-headed arrows indicate temporal changes in relative fitness.



CHAPTER 2

METHODS

Study Site and Nest Monitoring

Protection Island National Wildlife Refuge (48°07'40" N, 122°55'40" W) lies within Jefferson County, Washington, at the southeastern border of the Strait of Juan de Fuca. A low-lying gravel spit, Violet Point, extends approximately 1 km from the eastern side of the island. Violet Point typically hosts 2,500-3,000 breeding pairs of gulls; the colony is most dense around the marina, located at the western end of the spit, and along the south beach of the spit (Cowles and Galusha 2012).

From 27 May through 15 July 2011, five assistants and I monitored gull nests every evening (approximately 1700-2000 PST) within six sample plots around and north of the marina. We marked nests within the plots with a numbered wooden stake on the first evening they contained an egg; we searched plots thoroughly for new nests every evening. We labeled new eggs with a letter according to their order of appearance within the nest (a "typical" clutch consisted of A, B, and C eggs). We weighed each egg to the nearest 0.1 gram on the day that it appeared using an Ohaus Scout Pro SP401 Portable Scale. Every day we noted whether each egg was still present and intact or whether it had disappeared from the nest, hatched, was addled, did not complete pipping, or did not survive for some other reason. When possible, we recorded the fate of eggs that

disappeared or failed to hatch (e.g., eagle predation leaves telltale eggshells, some nests failed due to flood tides); when eggs disappeared singly from nests without leaving a trace, we assumed that gulls cannibalized them. We checked clutches for pipping eggs after the earliest surviving egg of the clutch had been present for 24 days. Once all chicks of the clutch hatched, we did not monitor the nest. I defined hatching success for a nest as the number of chicks hatched successfully from the nest regardless of the clutch size.

I mapped locations of all nests in the plots with a Trimble GeoExplorer 6000 series GeoXH handheld with an external Tornado antenna. Horizontal accuracy after differential correction was 10-14 cm for all GPS points. At the time of mapping, I designated each nest site as “sheltered” or “unsheltered.” I considered sheltered nests to be those that were placed next to a log taller than the nest, next to the “cliff” of the marina, or next to or in vegetation taller than the nest, often Gumweed (*Grindelia integrifolia*), American Dune Grass (*Leymus mollis*), or Silver Bur-weed (*Ambrosia chamissonis*). I considered unsheltered nests to be those that were not placed next to a structure taller than the nest, typically in short or sparse vegetation or on beach/marina cobblestones (see Appendix A for a more detailed explanation of the nest site categorization).

I was not able to obtain hatching success data for all nests; monitoring of late nests became too risky for chicks past 15 July, once they were several days old and mobile and thus vulnerable to chick cannibalism. These unfinished nests were followed long enough to be certain of clutch size; hence, analyses involving clutch size included both finished and unfinished nests, except for three that had complications necessitating their elimination from analysis: clutch size was probably inaccurate for one nest because

we ignored an egg found just outside of the nest; eggs in another nest were probably mislabeled, leading to doubt about the true clutch size; and I eliminated a third nest from analysis because a labeled egg from a different nest appeared in the nest. Analyses involving hatching success included only finished nests, excepting the three mentioned previously and two for which there was ambiguity in number of chicks hatched (e.g., the chick probably hatched but I was unable to find it or eggshells indicating that it hatched).

Assignment of Hybrid Indices

An assistant and I viewed individual 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). The index consisted of scores for back (mantle plus scapulars) shade, shade of primary tips, bill color, orbital ring color, and iris color. The assistant and I independently scored each character and averaged the scores if after discussion we could not agree. We obtained scores from 15 June through 14 July 2011 and only when cloud cover or fog rendered lighting conditions relatively consistent and good for observation of gray shades (Howell and Dunn 2007). We began data collection no earlier than 0700 PST and terminated it when the sunlight became bright enough to cause shadows (a solar radiation of roughly 300 W/m^2); most data collection occurred from 0800-1300 PST. We found that sunny conditions washed out differences in shades and made the angle at which the bird was standing to the sun impact the apparent shade. Under diffuse light this variation was much reduced, although we still made an effort to score plumage characters when the bird was broadside to us. When oriented parallel to our line of sight, feathers (especially primaries) appeared darker. We obtained character scores for individuals only when we

were positive to which territory the bird belonged, either because it was interacting with the nest or with a bird known to belong to that nest. We determined the gender of individuals by head morphology, overall size, and behavior. When uncertain, we did not make a final decision until both members of the pair were present, making the determination simple.

My assistant and I scored plumage characters according to a Kodak 20-step neutral gray scale (Color Separation Guide and Gray Scale [Small]; CAT 152 7654) because it is readily available and has been used by previous authors (Hoffman et al. 1978; Howell and Dunn 2007), although Bell (1996, 1997) and Good et al. (2000) used the Munsell scale. We scored bare part colors according to a 1-5 scale similar to that of Bell (1997) and Good et al. (2000); see Table 1. When scoring the primary tips, we compared the Kodak scale to those regions of the primary tips that were the least worn and bleached. I termed these original Kodak and bare part scores “raw character scores.”

Raw character scores were obtained for all characters of 169 pairs and an additional 16 males and 40 females, a total of 394 birds. All analyses pertaining solely to hybrid indices were carried out on this dataset. I obtained complete hybrid indices and complete nesting data (egg masses, clutch size, hatching success) for 147 pairs and an additional 13 males and 29 females.

Analysis

I converted the raw scores into “character scores” by rescaling the observed range of the raw scores equally from 1-10 (Table 1). The “observed range” included raw character scores from a pilot study conducted in 2010 because I wished to make the scores “comparable” across years. Thus, the actual range of wingtip scores for the 2011

data was 7 to 19, but I used a minimum value of 5 for wingtip score because that was the minimum value observed in 2010. I created a weighted index by adding the scaled (1-10) bare part scores to twice the sum of the scaled plumage scores:

$$\text{Hybrid Index} = 2(\text{back}) + 2(\text{wingtips}) + \text{beak} + \text{orbital ring} + \text{iris}.$$

All analyses reported here used these weighted hybrid indices, which are hereafter referred to as “hybrid indices.” I 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.” Note that, like the indices of Hoffman et al. (1978) but unlike those of Bell (1997) and Good et al. (2000), higher values of my index indicate “darker” or more Western Gull-like individuals.

In order to evaluate the hypothesis that the most common phenotype exhibits the greatest reproductive success, I calculated the “index distance to mode” (IDM) for each male, female, and pair index. For male and female hybrid indices, the index distance to mode is the absolute value of the difference between the index and the mode of the distribution of all indices. The mode of all indices was 29.5, thus:

$$\text{IDM} = | \text{index} - 29.5 |.$$

For pair indices, the IDM was calculated by:

$$\text{Pair IDM} = | \text{pair index} - 2(29.5) |.$$

Larger values of IDM represent individuals that are more like pure Glaucous-winged or Western gulls. Note that since the mode was closer to the Glaucous-winged end of the hybrid index range, individuals with the largest IDMs are Western-like individuals.

I used MATLAB with Statistics Toolbox (The MathWorks, Inc., Natick, Massachusetts) to conduct ordinal logistic regression and all statistical tests except Mann-Whitney U, which I performed in SPSS (IBM, Armonk, New York). I based my decision to use a parametric or nonparametric test for a given analysis on histograms and normal probability plots of the data. All tests were carried out at the $\alpha = 0.05$ significance level.

I used proportional odds model ordinal logistic regression (*mnrfit* in MATLAB) to test whether clutch size and hatching success were correlated with IDM or hybrid index (see Catry et al. 1999 for an example of ordinal logistic regression used in a similar context). Proportional odds model ordinal logistic regression yields odds ratios (ORs). An OR quantifies 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). I set $c = 10$ index units for analyses of male and female indices and IDMs. Because the range of the pair index is twice that of the individual indices, I set $c = 20$ index units for analyses of pair index and IDM.

Table 1. Scheme for conversion of raw scores to character scores (CS).

Back		Wingtips		Beak		Orbital Ring		Iris	
Kodak	CS	Kodak	CS	Color	CS	Color	CS	Color	CS
4.00	1.00	5.00	1.00	1 - Pale yellow	1.00	1 - Entirely pink	1.00	1 - Very dark brown	1.00
5.00	2.29	6.00	1.64	2 - Medium yellow	3.25	2 - Mostly pink	3.25	2 - Darkish brown	3.25
6.00	3.57	7.00	2.29	3 - Bright yellow	5.5	3 - Pink and yellow	5.5	3 - Medium brown	5.5
7.00	4.86	8.00	2.93	4 - Yellow-orange	7.75	4 - Mostly yellow	7.75	4 - Light yellowish	7.75
8.00	6.14	9.00	3.57	5 - Orange	10.00	5 - Entirely yellow	10.00	5 - Very pale yellowish	10.00
9.00	7.43	10.00	4.21						
10.00	8.71	11.00	4.86						
11.00	10.00	12.00	5.50						
		13.00	6.14						
		14.00	6.79						
		15.00	7.43						
		16.00	8.07						
		17.00	8.71						
		18.00	9.36						
		19.00	10.00						

CHAPTER 3

RESULTS

Colony Composition and Assortative Mating

Approximately 2,400 pairs of gulls nested on Violet Point in 2011 (Joe Galusha, personal communication); thus our sample of 394 birds contained 8% of the breeding gulls on Violet Point. Putatively pure individuals of both Glaucous-winged Gulls and Western Gulls occurred on the colony. However, Glaucous-winged Gulls and/or Glaucous-winged Gull-like hybrids dominated the colony, although relatively few exhibited the “classic” Glaucous-winged extremely pale wingtips (Fig. 2). Table 2 lists descriptive statistics for the raw character scores of all males and females observed. Plumage character scores and indices were not significantly different between genders, but beak and orbital ring scores were significantly higher for males and iris scores were significantly higher for females (Table 3).

The hybrid indices of males and females from pairs were significantly directly correlated ($r = 0.35$, $p = 0.000003$); however, when the three pairs that exhibited the highest pair index were not included, the relationship was non-significant ($r = 0.10$, $p = 0.21$; Fig. 3). Individual character scores of males and females in pairs were significantly directly correlated, except for iris scores (Table 4).

Nest Site Choice and Reproductive Success

Male index, female index, and pair index were not significantly different for sheltered and unsheltered nests; however, pair index was close to significantly different (Table 5). Male, female, and pair IDMs also were not significantly different for sheltered and unsheltered nests (Table 6). A, B, and C egg masses were not significantly different across habitats (Table 7). Fourth, fifth, and sixth (D, E, and F) eggs accounted for only 1% of the data and thus were not included in analyses of egg mass. Clutch size and hatching success were significantly different across habitats, with sheltered nests having larger clutch sizes and greater hatching success (Table 8). The main driver of decreased success for unsheltered nests was egg cannibalism: 14% of finished eggs in sheltered nests were cannibalized, whereas 27% of finished eggs in unsheltered nests were cannibalized.

A and B egg masses were not significantly correlated with male index, female index, or pair index; however, C egg mass was significantly negatively correlated with pair index and trended with male index and female index, although these latter two relationships were not significant (Table 9). Thus, C eggs of Western Gull-like individuals tend to be smaller than C eggs of Glaucous-winged Gull-like individuals. A, B, and C egg masses were not significantly correlated with IDM, although the correlation for C egg mass with pair IDM was close to significant (Table 10).

Clutch size and hatching success were not significantly correlated with male, female, or pair hybrid index, although p-values for pair index with clutch size and female index with hatching success approached significance at the 90% confidence level with Western Gull-like individuals tending to experience greater reproductive success (Table

11). Clutch size and hatching success were not significantly correlated to male, female, or pair IDM, although the p-value for female index with hatching success approached significance at the 90% confidence level with individuals most unlike the modal phenotype tending to experience greater reproductive success (Table 12).

Table 2. Descriptive statistics for raw character scores of all males (n = 185) and females (n = 209) observed.

	Average	SD
Males		
Back	7.35	0.66
Wingtips	12.35	2.23
Beak	2.84	0.91
Orbital ring	1.83	1.17
Iris	2.14	1.02
Females		
Back	7.32	0.73
Wingtips	12.56	2.35
Beak	2.48	1.03
Orbital ring	1.49	0.94
Iris	2.77	1.08

Table 3. Average character scores and hybrid indexes for males (n = 185) and females (n = 209) and p-values for differences in these scores between males and females (two-tailed Mann-Whitney U).

	♂ Avg	♀ Avg	p
Back	5.31	5.27	0.673
Wingtips	5.73	5.86	0.246
Beak	5.14	4.34	<0.001
Orbital ring	2.86	2.10	<0.001
Iris	3.55	4.97	0.001
Index	33.62	33.66	0.902

Table 4. Pearson's correlation coefficients and p-values for relationships between character scores of paired males and females (n = 169).

	r	p
Back	0.369	<0.0001
Wingtips	0.305	0.0001
Beak	0.267	0.0005
Orbital ring	0.399	<0.0001
Iris	0.109	0.1568

Table 5. Average value of hybrid indices for sheltered and unsheltered nests and p-values for differences in indices between the site types (two-tailed Mann-Whitney U).

	Average	n	p
Males			
Sheltered	34.12	126	0.441
Unsheltered	32.75	69	
Females			
Sheltered	33.81	125	0.910
Unsheltered	33.42	84	
Pairs			
Sheltered	68.15	115	0.061
Unsheltered	64.99	54	

Table 6. P-values for differences in index distance to mode (IDM) between sheltered and unsheltered nest sites (two-tailed Mann-Whitney U).

	n	p
Males		
Sheltered	126	0.712
Unsheltered	69	
Females		
Sheltered	125	0.720
Unsheltered	84	
Pairs		
Sheltered	115	0.158
Unsheltered	54	

Table 7. Average egg masses from sheltered and unsheltered nests and p-values for differences in egg mass between the nest types (two-tailed independent t-test).

	Average (g)	n	p
A eggs			
Sheltered	95.98	149	0.355
Unsheltered	94.99	76	
B eggs			
Sheltered	95.06	146	0.221
Unsheltered	93.71	74	
C eggs			
Sheltered	90.58	122	0.705
Unsheltered	91.05	51	

Table 8. Average clutch size and hatching success for sheltered and unsheltered nests and p-values for differences in clutch size or hatching success between the nest types (two-tailed Mann-Whitney U).

	Average	n	p
Clutch size			
Sheltered	2.82	152	0.014
Unsheltered	2.64	76	
Hatching success			
Sheltered	2.2	130	<0.001
Unsheltered	1.72	64	

Table 9. Pearson correlation coefficients and p-values for relationships between hybrid indices and egg masses.

	A eggs			B eggs			C eggs		
	r	p	n	r	p	n	r	p	n
Male index	0.028	0.711	181	0.021	0.777	178	-0.110	0.194	141
Female index	0.003	0.963	203	0.013	0.860	200	-0.128	0.106	160
Pair index	0.010	0.903	165	-0.004	0.957	164	-0.178	0.041	133

Table 10. Pearson correlation coefficients and p-values for relationships between index distance to mode (IDM) and egg mass.

	A eggs			B eggs			C eggs		
	r	p	n	r	p	n	r	p	n
Male IDM	-0.024	0.747	181	-0.009	0.902	178	-0.109	0.198	141
Female IDM	-0.010	0.891	203	-0.013	0.853	200	-0.107	0.175	160
Pair IDM	-0.007	0.925	165	-0.039	0.621	164	-0.161	0.064	133

Table 11. Coefficients (β) and their standard errors (SE) and p-values, odds ratios (OR), and 95% confidence intervals (CI) for the ORs for ordinal logistic regression of clutch size and number hatched with hybrid indices.

	β^a	SE ^b	p	c	OR	95% CI		n
Clutch size								
Male index	0.029	0.027	0.279	10	1.34	0.79	2.27	183
Female index	0.029	0.027	0.279	10	1.34	0.79	2.27	206
Pair index	0.035	0.023	0.131	20	2.01	0.81	4.97	167
Number hatched								
Male index	0.015	0.021	0.470	10	1.16	0.78	1.73	160
Female index	0.031	0.019	0.103	10	1.37	0.94	1.99	176
Pair index	0.017	0.013	0.192	20	1.41	0.84	2.37	147

^a Reversed signs on the betas outputted from MATLAB so that $OR > 1$ corresponds to increasing success as the index increases.

^b Dispersion estimated.

Table 12. Coefficients (β) and their standard errors (SE) and p-values, odds ratios (OR), and 95% confidence intervals (CI) for the ORs for ordinal logistic regression of clutch size and number hatched with index distance to mode (IDM).

	β^a	SE ^b	p	c	OR	95% CI		n
Clutch size								
Male IDM	0.048	0.036	0.186	10	1.62	0.79	3.31	183
Female IDM	0.037	0.032	0.255	10	1.45	0.77	2.72	206
Pair IDM	0.018	0.022	0.435	20	1.42	0.59	3.43	167
Number hatched								
Male IDM	0.018	0.025	0.463	10	1.20	0.74	1.96	160
Female IDM	0.035	0.023	0.125	10	1.42	0.91	2.22	176
Pair IDM	0.012	0.015	0.399	20	1.28	0.72	2.29	147

^a Reversed signs on the betas outputted from MATLAB so that OR > 1 corresponds to increasing success as the index increases.

^b Dispersion estimated.

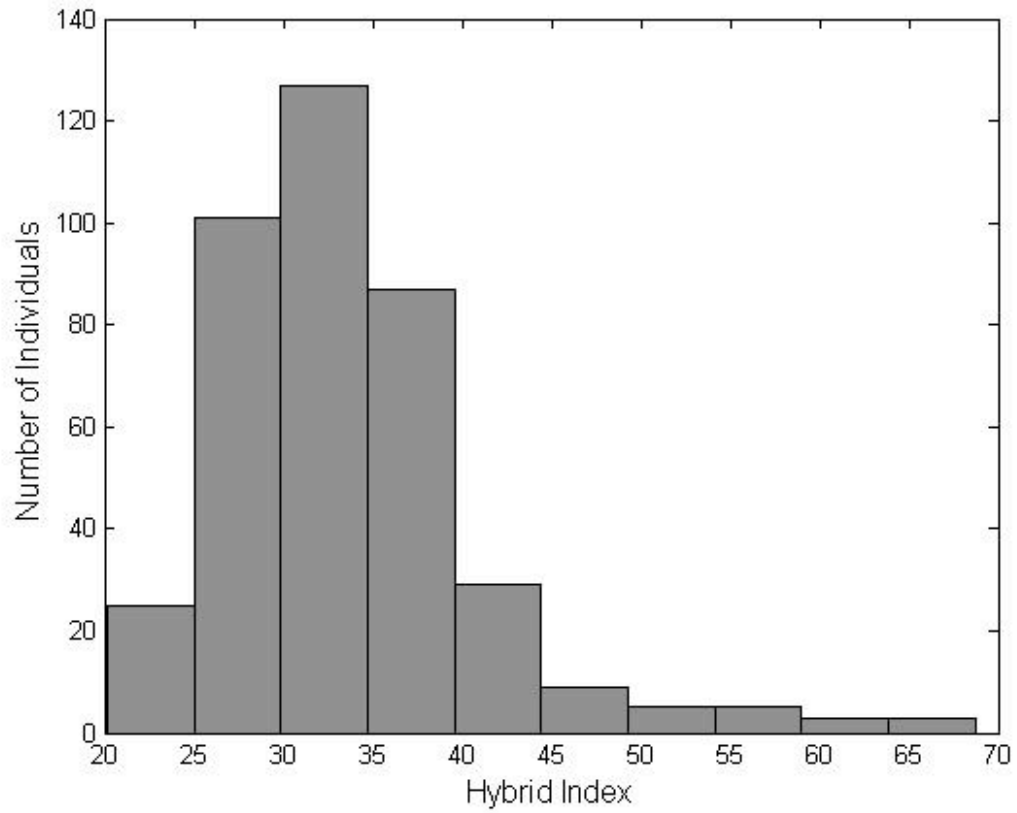


Fig. 2. Frequency distribution of hybrid indices for all individuals observed (n = 394). Higher values of the index represent more Western Gull-like individuals.

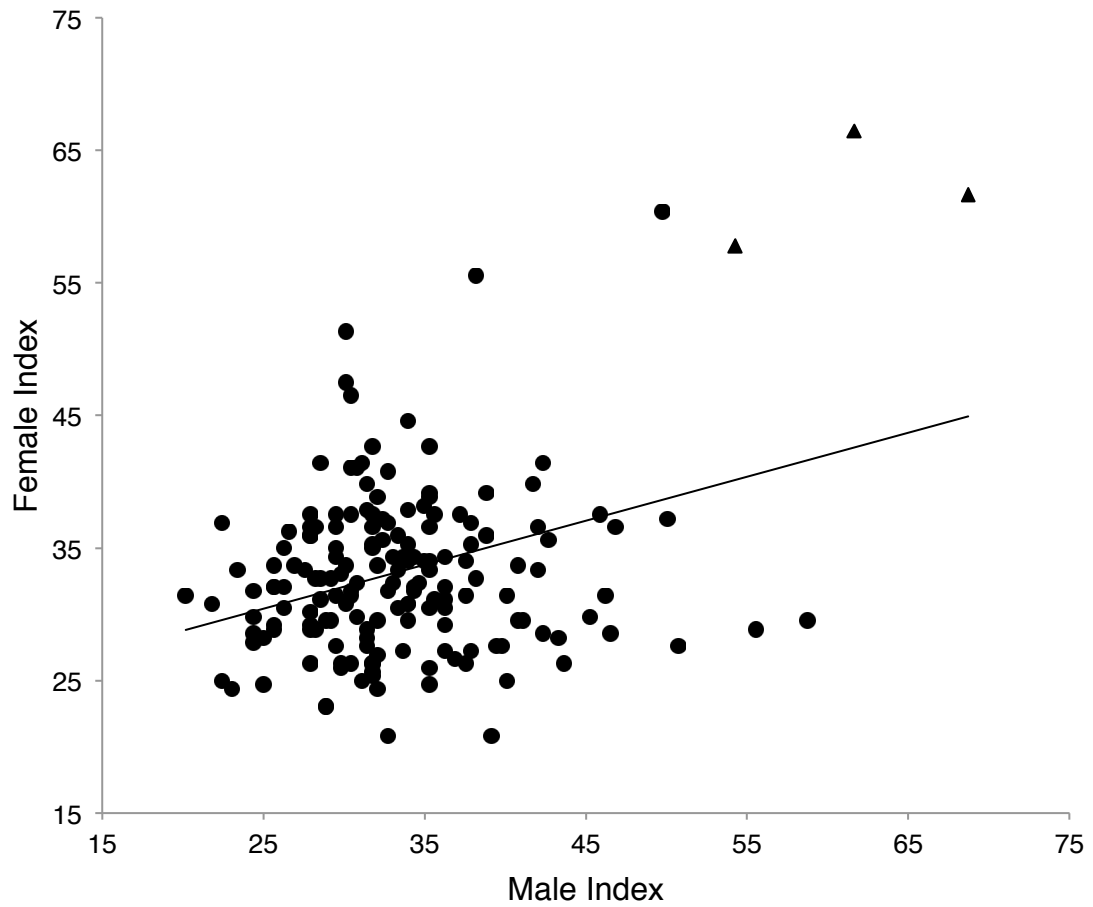


Fig. 3. Correlation of hybrid indices between males and females of pairs ($n = 169$). This relationship is significant ($r = 0.35$, $p < 0.0001$). If the three pairs denoted by triangles are removed (those with the three highest pair indices), however, the relationship becomes non-significant ($r = 0.10$, $p = 0.21$). Higher values of the index represent more Western Gull-like individuals. Linear trendline for all data is shown.

CHAPTER 4

DISCUSSION

Methodology

My hybrid index values are not directly comparable to those obtained in previous work due to differences in methodology and in the gray scales used; even small differences in the methodology for obtaining hybrid indices can produce a noticeable effect. For example, in a pilot study for my thesis in 2010, my assistant and I did not use the spotting scope to find the least bleached and worn areas of the wingtips; this led to artificially lighter wingtip scores (A. E. Moncrieff unpubl. data). Previous authors gave no indication that their methodologies accounted for bleaching and wear of the feathers. I believe that my methodology accurately described relative differences in phenotypic characters of gulls in the Protection Island colony. Indices were made more rigorous by use of independent assessment by two observers; furthermore, my assistant and I were able to replicate results and identify birds based on raw character scores at later dates.

Previous authors (Bell 1997; Good et al. 2000) did not scale their raw character scores; instead they simply added the bare part scores, which had smaller ranges, to the plumage scores, causing the plumage characters to have greater influence on the hybrid index. Hybrid indices have been constructed this way because plumage scores are more effective discriminators of pure and hybrid individuals, although inclusion of bare part

scores enhances the discrimination (Bell 1996). My method of weighting the hybrid index is not directly equivalent to that of previous authors, but I believe it is a more reasonable way of constructing the hybrid index because it weights the scores in a controllable way.

Hybrid indices spanned a continuous range. Because no work has been done to define *L. glaucescens*, *L. occidentalis*, and their hybrids in terms of Kodak scores, I chose analytic methods that did not require construction of artificial categories. Thus, instead of referring to individuals as “Glaucous-winged Gulls” I refer to individuals as “Glaucous-winged Gull-like” if their indices placed them towards the low end of my hybrid index; these individuals may in actuality be either pure *L. glaucescens* or hybrids.

Colony Composition and Assortative Mating

Bell (1996) collected 17 birds from Protection Island and used canonical discriminant function analysis of colorimetric characters to determine that eight were Glaucous-winged Gulls, one was a Western Gull, and eight were hybrids. The frequency distribution of my 394 birds roughly corresponds to this: the vast majority are Glaucous-winged Gulls and/or their hybrids—potentially, there are about as many Glaucous-winged Gulls as there are hybrids, depending on how one defines the categories—with relatively few Western Gull-like birds (Fig. 2).

As did Hoffman et al. (1978) and Bell (1997), I found a strong tendency for individuals to pair with mates having a similar phenotype; however, the statistical significance of this relationship was driven entirely by a few Western Gull-like pairs. Individuals with intermediate and Glaucous-winged Gull-like hybrid indices did not necessarily pair with individuals very like themselves, although they did typically pair

with other intermediate or Glaucous-winged Gull-like individuals. I noticed only one pair in which the individuals looked very dissimilar: an intermediate male paired with a Western Gull-like female.

Nest Site Choice and Reproductive Success

Mass of the third egg of a clutch is used as a measure of success, because chicks from smaller eggs are less likely to survive and 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 and second eggs of the clutch (Pierotti and Bellrose 1986). Reported egg masses for Western and Glaucous-winged Gulls are similar (Verbeek 1986; Pierotti and Annett 1995), so I assume that trends in my data are due to female condition rather than species differences. Western Gull-like individuals on Protection Island had smaller third eggs, and thus by this indicator were less successful than hybrids and Glaucous-winged Gulls. Egg mass is a relatively minor measure of fitness, however, and this trend of decreased Western Gull success did not hold for more direct measures of success, namely clutch size and hatching success.

I found that sheltered nests contained larger clutch sizes and exhibited better hatching success; this has been the case for the Protection Island colony during previous years (J. L. Hayward unpubl. data). Because hybrid indices and IDMs are not different for the two site types, however, there is no evidence that any particular phenotype is capitalizing on this. In Grays Harbor, Washington, hybrids were more successful than Western Gulls because they chose vegetated (sheltered) nest sites (Good et al. 2000; see also Good 2002). In contrast, Western Gull-like individuals on Protection Island did not tend to choose unsheltered nest sites. Of the 10 pairs with the greatest hybrid indices,

seven chose sheltered nest sites; six of these were sheltered by vegetation. If the non-significant trends identified by the odds ratios for relationships between hybrid indices and reproductive success actually are reflective of some biological difference, it is possible that the close-to-significant ($p = 0.061$) difference in hybrid index for sheltered and unsheltered nest sites explains the tendency for Western Gull-like birds to have greater success. It should be noted, however, that the average pair indices for the two nest site types differ by four index units; I hesitate to assign biological significance to such a small difference. Alternatively, it is possible that Western Gull-like individuals differed in diet choice, which increased clutch size and hatching success; Good et al. (2000) found evidence for this effect among hybrids on Tatoosh Island. Diet choice is known to affect reproductive success in both Western and Glaucous-winged Gulls (Murphy et al. 1984; Annett and Pierotti 1999).

Limitations

It is likely that my sample of gulls was not truly random. Although I tried to obtain character scores for all birds within our six study plots, I was not able to obtain scores for all birds: wary birds flew at my approach. Thus my sample is biased towards tamer birds. There also was bias against certain nest site types—it was harder to obtain character scores for birds nesting in tall dune grass (*Leymus mollis*) because (1) they could not be observed while sitting on the nest and (2) once they were displaced from the nest they tended to be wary of approach. Furthermore, 57% of the nests for which I obtained character scores for one or both members of the pair occurred in two of six study plots. A six-year study of reproductive success on Protection Island has demonstrated that different plots, or sub-regions of the colony, experience different

pressures (e.g., amount of eagle predation or egg cannibalism) and have differential hatching success (J. L. Hayward unpubl. data). Because the gulls were not banded, I had to include only those that were actively nesting so I could identify individuals based on which nest they tended. I did not begin collecting character scores until most birds on the colony were well into egg-laying or beginning incubation, so early nesters that abandoned before my study began were not included in the sample. Thus, it is very possible that my sample is biased towards more successful gulls and did not capture the entire range of success outcomes experienced by the birds.

I was unable to follow chicks through to fledging and thus cannot comment on whether the gulls might experience differential fledging success. Following chicks for the first week or two after hatching could yield interesting results, given that many chicks die in the first week or two when they are small enough to be easily grabbed by neighboring adult gulls. It is likely that chicks from unsheltered nests experience greater mortality in this manner than those from sheltered nests. It should be noted, however, that I found no strong correlation between hybrid index and habitat choice; thus, obtaining data on chick survival may not settle the question of hybrid superiority. Indeed, Good et al. (2000) found that when hybrids experienced greater hatching success, they also experienced greater fledging success.

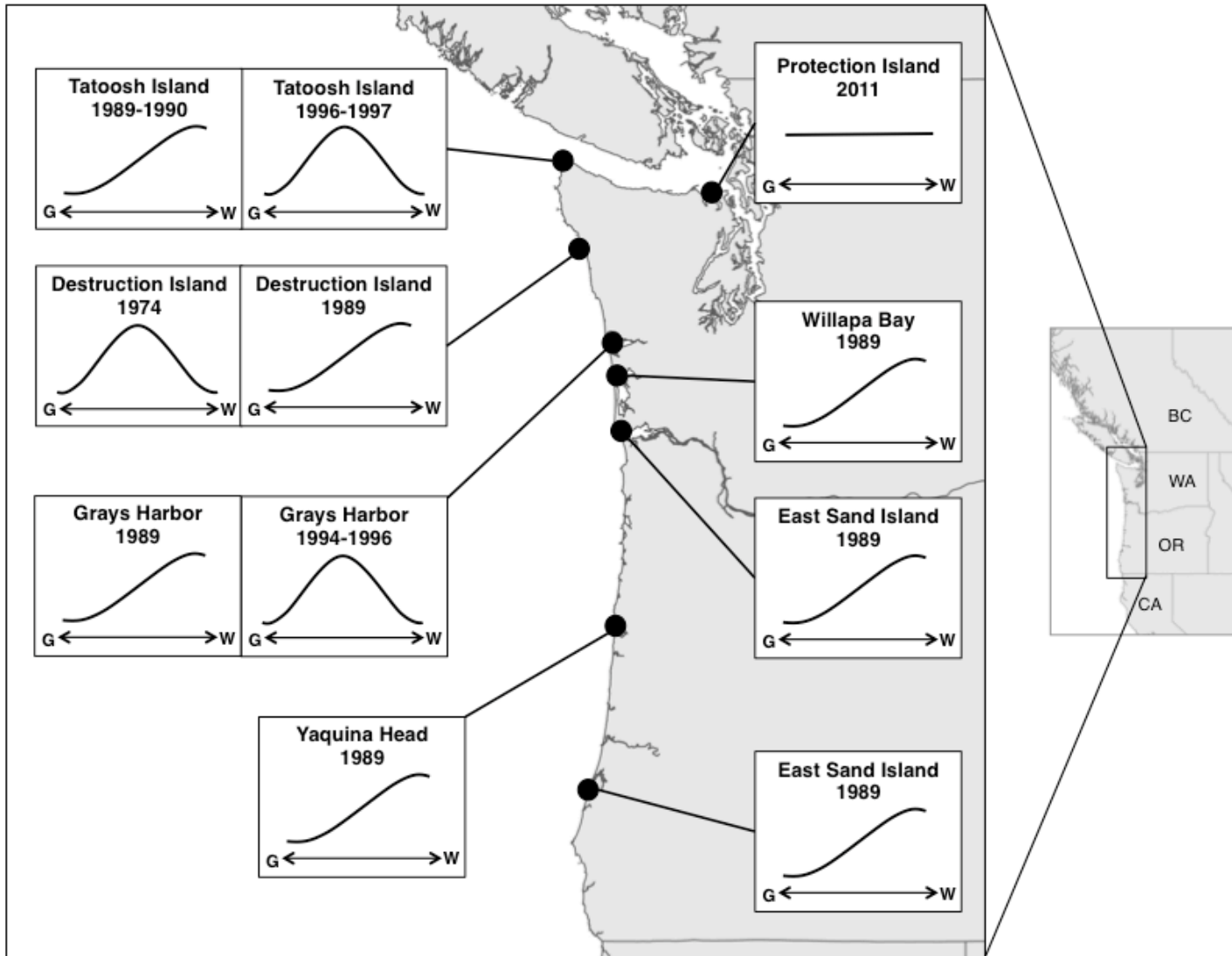
Conclusions

I found no evidence of differential habitat choice according to phenotype, and reproductive success was not significantly greater for the most common phenotype on the colony or for pure Glaucous-winged or pure Western individuals. This result does not support the dynamic-equilibrium hypothesis, which postulates that hybrids always

experience the least success. It also does not support the bounded hybrid superiority hypothesis, which predicts that (1) if the colony is within the zone of hybrid superiority, hybrids experience the greatest success, and that (2) north of the hybrid zone, Glaucous-winged Gulls are most successful. It is possible that Protection Island is on or near the boundary between hybrid superiority and Glaucous-winged Gull superiority, and thus neither hybrids nor Glaucous-winged Gulls were most successful. This explanation fails to account, however, for the fact that Western Gull-like individuals experienced the same relative success as intermediates and Glaucous-winged Gull-like birds: There are no apparent fitness consequences for Western Gulls at the northern end of the hybrid zone. It is also possible that a selection-hybridization balance is operating; I do not have rigorous data for multiple years for the Protection Island colony, and so I cannot comment upon whether success varies for phenotypes across years. (However, limited data from a 2010 pilot study also showed no significant relationship between hybrid index and clutch size or hatching success.) It is known that Protection Island gulls experience decreased success during El Niño years (J. L. Hayward unpubl. data); determining whether success differs according to hybrid index under those conditions could be informative.

Evidence to date regarding relative fitness of hybrids and parental types within the zone are summarized in Figure 4. Without data from multiple years for several colonies across the zone, it is unclear which model of the hybrid zone is most accurate.

Fig. 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. Map credit: Esri, DeLorme Publishing Company, Inc.



APPENDIX A

DETAILED NEST HABITAT CATEGORIES

Table 13. Acronyms for and descriptions of original nest site categories.

Acronym	Description
Sheltered	
BS	Beside shrub; often Gumweed (<i>Grindelia integrifolia</i>), Silver Bur-weed (<i>Ambrosia chamissonis</i>) or tall clump of (non-Dune) grass
CC	On cobbles up against the gravel bank of the marina
LB	Next to a log (or logs) on the beach
LN	Next to a log (or logs) away from the beach
TE	At the edge of Dune Grass (<i>Leymus mollis</i>)
TT	At the end of a tunnel into Dune Grass
Unsheltered	
CN	On cobbles of the beach or marina but not up against a gravel bank
SV	In short vegetation, i.e. vegetation that was not much taller than the nest rim and didn't provide cover for the nest

APPENDIX B

HISTOGRAMS AND NORMAL PROBABILITY PLOTS

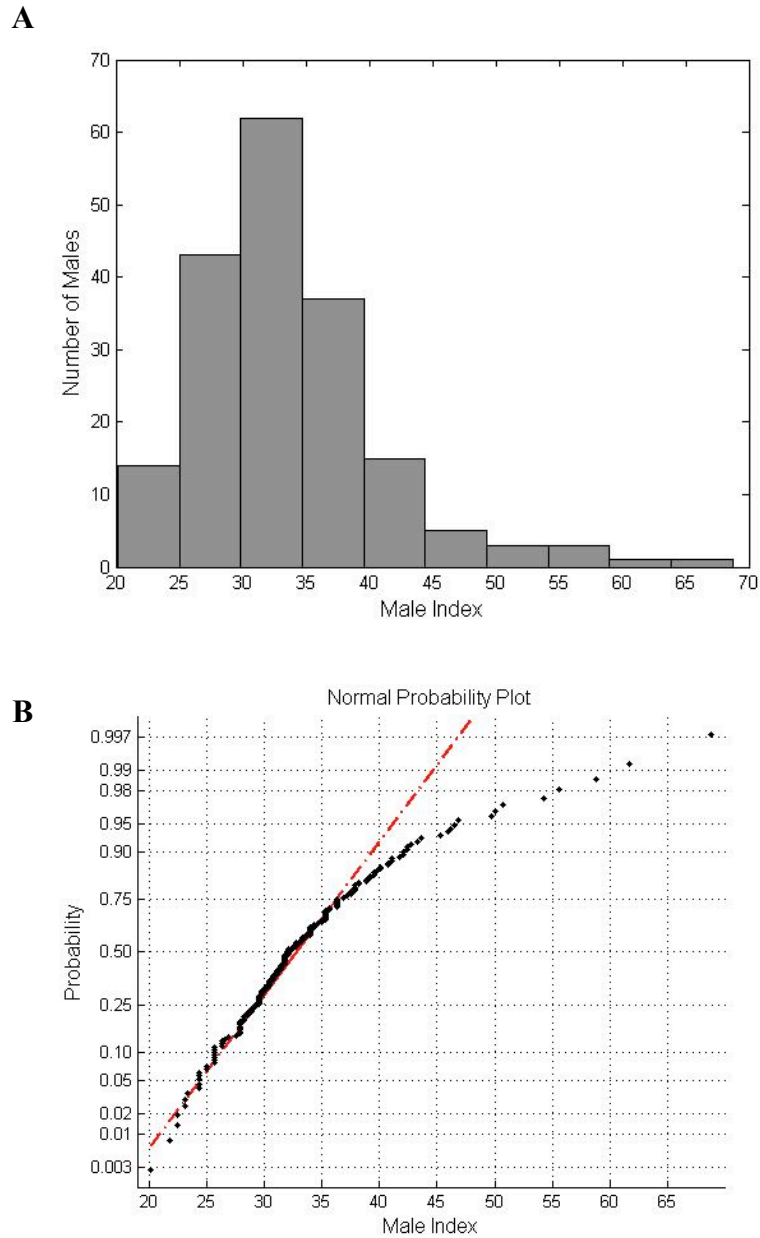


Fig. 5. Histogram and normal probability plot for male index data ($n = 185$). I determined that male index data were not normally distributed by examining (A) a histogram and (B) a normal probability plot of the data. Normally distributed data should be symmetric about the mode in a histogram and should fall along the dashed line in a normal probability plot.

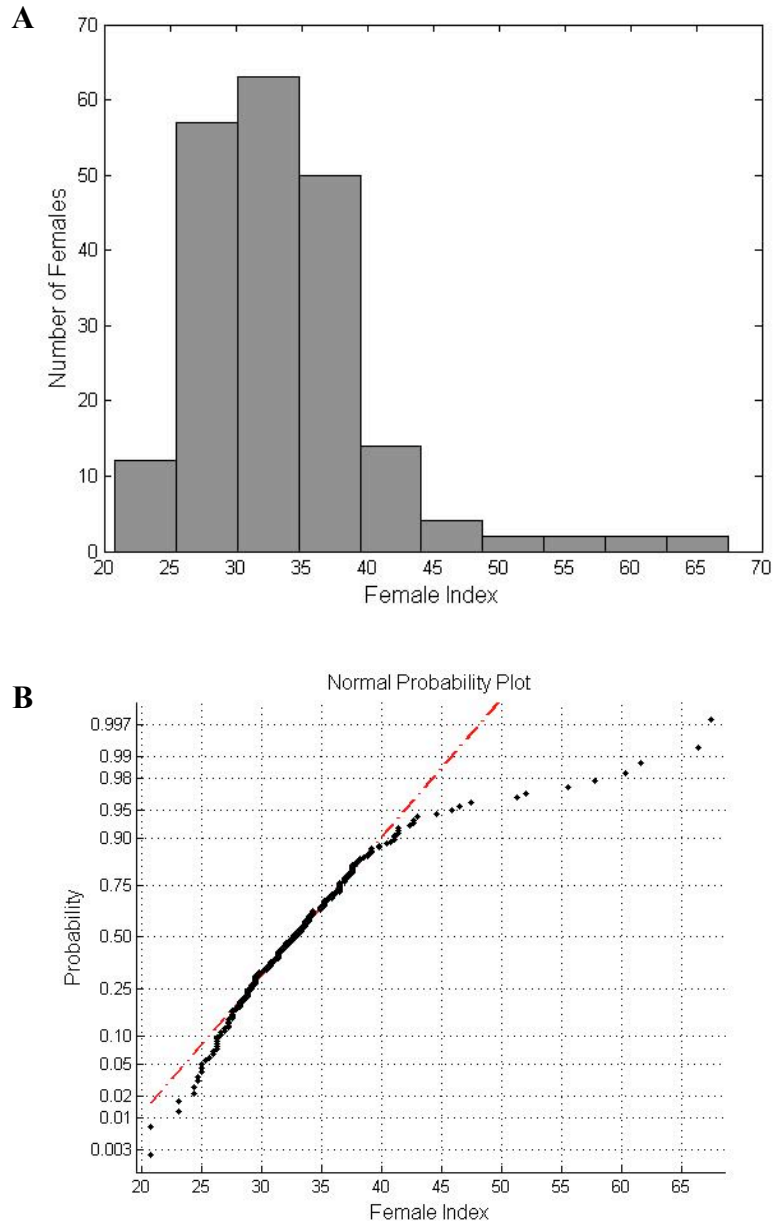
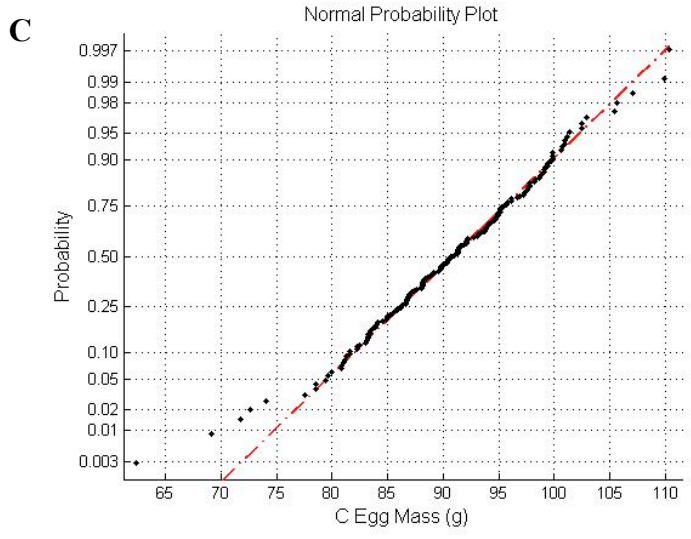
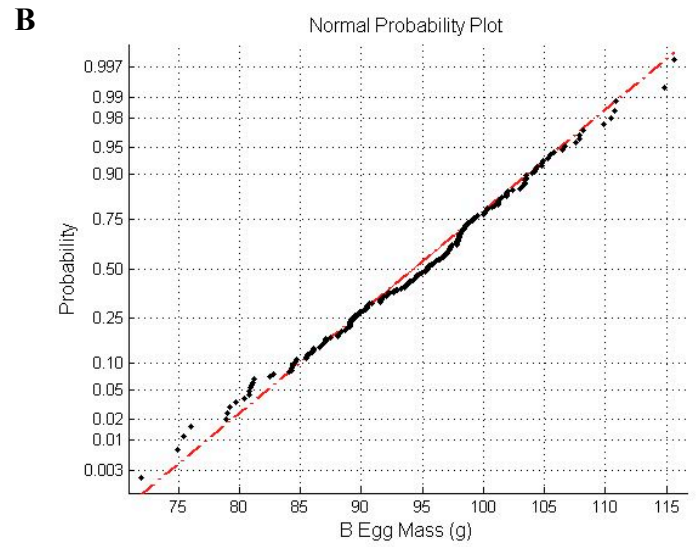
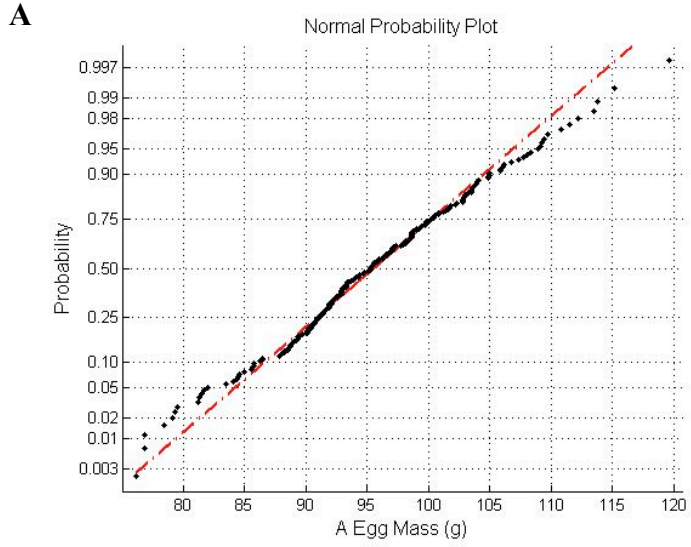


Fig. 6. Histogram and normal probability plot for female index data ($n = 209$). I determined that female index data were not normally distributed by examining (A) a histogram and (B) a normal probability plot of the data. Normally distributed data should be symmetrical about the mode in a histogram and should fall along the dashed line in a normal probability plot.

Fig. 7. Normal probability plots for A, B, and C egg masses (n = 225, 220, and 174, respectively). I determined that the **(A)** A egg masses, **(B)** B egg masses, and **(C)** C egg masses were normally distributed by examining normal probability plots. Normally distributed data should fall along the dashed line.



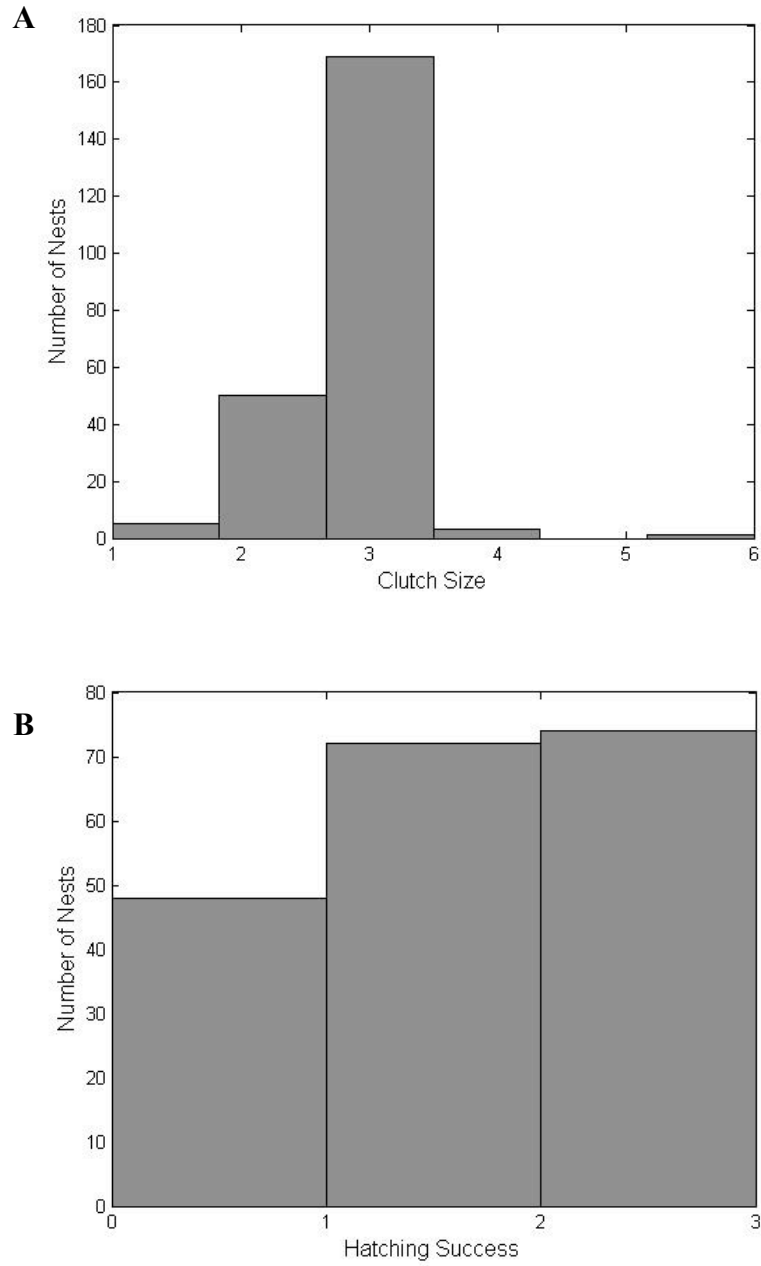


Fig. 8. Histograms for clutch size ($n = 228$) and hatching success ($n = 194$). I determined that **(A)** clutch size and **(B)** hatching success data were not normally distributed by examining histograms of the data. Normally distributed data should be symmetric around the mode.

APPENDIX C

ORDINAL LOGISTIC REGRESSION

Logistic regression is employed for binary outcomes (0 or 1). In contrast, ordinal logistic regression admits multiple, rank-ordered outcomes. My data consisted of ordered reproductive success outcomes (i.e., clutch size or number of chicks hatched) that I wished to regress on hybrid index or index distance to mode (IDM).

Following the notation of Hosmer and Lemeshow (2000), consider a system with $K + 1$ ordered outcomes denoted $0, 1, 2, \dots, K$. Let $\phi_k(x)$ denote the probability that outcome Y is equal to k given the hybrid index (or IDM) x . The log of the proportional odds, which compares the probability of an equal or smaller response to the probability of a larger response, is regressed on the hybrid index (or index distance) x :

$$\ln \left[\frac{P(Y \leq k | x)}{P(Y > k | x)} \right] = \ln \left[\frac{\phi_0(x) + \phi_1(x) + \dots + \phi_k(x)}{\phi_{k+1}(x) + \phi_{k+2}(x) + \dots + \phi_K(x)} \right] = \beta_0 - \beta_1 x,$$

or equivalently,

$$\ln \left[\frac{P(Y > k | x)}{P(Y \leq k | x)} \right] = -\beta_0 + \beta_1 x.$$

(MATLAB estimates of β_0 and β_1 are based on the former equation, but I changed the signs of the estimated β_0 and β_1 in Tables 11 and 12 because the latter formulation is easier to interpret in my context.)

The likelihood function is

$$l(\beta_0, \beta_1) = \prod_{i=1}^n \left[\phi_0(x_i)^{z_{0i}} \phi_1(x_i)^{z_{1i}} \times \dots \times \phi_K(x_i)^{z_{Ki}} \right]$$

(Hosmer and Lemeshow 2000) and the log-likelihood is

$$L(\beta_0, \beta_1) = \sum_{i=1}^n \left[z_{0i} \ln[\phi_0(x_i)] + z_{1i} \ln[\phi_1(x_i)] + \dots + z_{Ki} \ln[\phi_K(x_i)] \right],$$

where $z_{ji} = 1$ when $y = j$ and $z_{ji} = 0$ otherwise. I maximized $L(\beta_0, \beta_1)$ numerically using the *mnrfit* function, adjusted for overdispersion, in MATLAB. Overdispersion occurs when

the sampling variance exceeds the theoretical variance and can result from a lack of independence in individual responses. The MATLAB overdispersion correction adjusts confidence intervals and p-values to account for increased uncertainty.

If x increases by c units, the odds ratio (OR) quantifies the change in the proportional odds:

$$OR = \frac{P(Y \leq k | x + c) / P(Y > k | x + c)}{P(Y \leq k | x) / P(Y > k | x)}.$$

The log of the odds ratio for a change of c in x , from x to $x + c$, is thus

$$\begin{aligned} \ln(OR) &= \ln \left[\frac{P(Y \leq k | x + c)}{P(Y > k | x + c)} \right] - \ln \left[\frac{P(Y \leq k | x)}{P(Y > k | x)} \right] \\ &= [\beta_0 - (x + c)\beta_1] - (\beta_0 - x\beta_1) = -c\beta_1. \end{aligned}$$

The odds ratio is thus

$$OR = e^{-c\beta_1}.$$

The 95% confidence interval (CI) for the odds ratio is obtained by

$$CI = e^{-c(\beta_1 \pm 1.96SE)},$$

where 1.96 is the z-score for the 95% confidence level and SE is the standard error of the coefficient β_1 . When the confidence interval brackets 1, the odds ratio and β_1 are not significant at the 95% confidence level. If the confidence interval lies entirely above 1, the odds of having an outcome $Y \leq k$ for $x + c$ are significantly greater than the odds of having an outcome $Y \leq k$ for x .

The proportional odds model assumes that the log odds are independent of outcome category. This assumption can be tested using the likelihood ratio comparison

$$G = -2[\text{L}_{\text{proportional odds model}} - \text{L}_{\text{multinomial model}}]$$

with degrees of freedom $((K+1)-2)p$, where p is the number of covariates. The G statistic has a chi-square distribution. If the proportional odds assumption holds the log-likelihoods will not be significantly different. The assumption holds for my study (see Tables 14 and 15).

Table 14. Results of likelihood ratio comparison test for ordinal logistic regression of hybrid index and clutch size or hatching success.

	G	p
Clutch size ^a		
Male index	3.49	0.62
Female index	5.49	0.36
Pair index	5.77	0.33
Number hatched ^b		
Male index	0.11	0.95
Female index	1.81	0.40
Pair index	1.17	0.56

^a d.f. = 5, $G_{crit} = 11.07$ at the 95% confidence level.

^b d.f. = 2, $G_{crit} = 5.99$ at the 95% confidence level.

Table 15. Results of likelihood ratio comparison test for ordinal logistic regression of index distance to mode (IDM) and clutch size or hatching success.

	G	p
Clutch size ^a		
Male IDM	-75.22	1
Female IDM	2.88	0.72
Pair IDM	-195.52	1
Number hatched ^b		
Male IDM	1.03	0.60
Female IDM	1.48	0.48
Pair IDM	0.22	0.90

^a d.f. = 5, $G_{crit} = 11.07$ at the 95% confidence level.

^b d.f. = 2, $G_{crit} = 5.99$ at the 95% confidence level.

APPENDIX D

RAW DATA

Table 16. Character scores and hybrid indexes.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
001	10.00	9.36	10.00	10.00	10.00	68.71	8.71	9.36	10.00	10.00	5.50	61.64	130.36
004	6.14	5.50	5.50	3.25	5.50	37.54	6.14	4.86	5.50	1.00	5.50	34.00	71.54
005	4.86	5.18	1.00	1.00	1.00	23.07							
010	6.14	6.14	5.50	1.00	1.00	32.07	5.50	3.25	5.50	1.00	5.50	29.50	61.57
012	4.21	3.57	5.50	5.50	3.25	29.82							
013	5.50	6.79	5.50	10.00	1.00	41.07							
022							6.14	4.86	5.50	1.00	5.50	34.00	
024	6.14	7.11	5.50	3.25	5.50	40.75	4.86	6.14	1.00	1.00	5.50	29.50	70.25
026	4.86	3.89	5.50	1.00	1.00	25.00	4.86	5.50	3.25	1.00	3.25	28.21	53.21
027	4.86	5.18	5.50	5.50	3.25	34.32	4.21	6.79	1.00	1.00	7.75	31.75	66.07
028	4.86	6.79	5.50	3.25	1.00	33.04	4.86	4.21	5.50	5.50	3.25	32.39	65.43
033	4.86	6.79	5.50	3.25	5.50	37.54	4.21	5.50	5.50	1.00	5.50	31.43	68.96
034	4.86	4.86	5.50	10.00	3.25	38.18	7.43	8.71	7.75	10.00	5.50	55.54	93.71
035							4.86	4.86	3.25	5.50	3.25	31.43	
037	6.14	4.86	5.50	1.00	3.25	31.75	6.14	5.50	5.50	1.00	5.50	35.29	67.04
041	4.86	6.14	5.50	1.00	3.25	31.75	4.86	6.79	1.00	1.00	1.00	26.29	58.04
042	3.57	4.86	1.00	1.00	5.50	24.36	4.21	3.57	3.25	1.00	10.00	29.82	54.18
043	4.21	4.86	5.50	3.25	5.50	32.39	4.86	8.07	3.25	1.00	5.50	35.61	68.00
044							6.14	5.82	1.00	3.25	10.00	38.18	
045	6.14	6.14	5.50	3.25	5.50	38.82	6.14	7.43	5.50	1.00	5.50	39.14	77.96
047	4.86	4.21	5.50	1.00	1.00	25.64	4.86	4.86	5.50	3.25	5.50	33.68	59.32
048							8.71	10.00	10.00	10.00	10.00	67.43	
049	6.14	5.50	5.50	5.50	5.50	39.79	4.86	5.18	1.00	3.25	3.25	27.57	67.36
050	4.86	4.21	5.50	1.00	3.25	27.89	4.86	6.79	5.50	1.00	7.75	37.54	65.43
052							5.50	4.86	5.50	1.00	1.00	28.21	

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
053	4.86	6.79	5.50	5.50	1.00	35.29	4.86	5.50	3.25	1.00	1.00	25.96	61.25
054	4.86	6.79	1.00	1.00	5.50	30.79	6.14	6.14	5.50	5.50	5.50	41.07	71.86
055	4.86	6.14	5.50	3.25	1.00	31.75	6.14	8.07	5.50	3.25	5.50	42.68	74.43
057	4.86	4.21	5.50	3.25	3.25	30.14	4.86	4.86	7.75	1.00	5.50	33.68	63.82
058							4.86	6.14	1.00	1.00	5.50	29.50	
060	5.50	5.50	5.50	1.00	7.75	36.25	4.86	3.57	5.50	3.25	5.50	31.11	67.36
061	5.50	6.14	5.50	1.00	3.25	33.04	5.50	6.79	5.50	1.00	3.25	34.32	67.36
063							6.14	7.43	5.50	1.00	3.25	36.89	
064							4.21	5.50	5.50	3.25	5.50	33.68	
066							4.86	7.43	5.50	1.00	10.00	41.07	
067	6.14	6.79	10.00	3.25	7.75	46.86	6.14	6.14	5.50	5.50	1.00	36.57	83.43
068	5.50	4.86	5.50	5.50	5.50	37.21	5.50	6.14	7.75	1.00	5.50	37.54	74.75
069							4.86	6.79	3.25	1.00	5.50	33.04	
073	4.21	4.21	5.50	1.00	1.00	24.36							
075	5.50	4.86	5.50	1.00	3.25	30.46	6.14	5.50	7.75	1.00	5.50	37.54	68.00
077	4.86	4.86	5.50	3.25	3.25	31.43	4.21	3.57	5.50	1.00	5.50	27.57	59.00
078	6.14	4.86	5.50	1.00	1.00	29.50	6.14	6.14	1.00	1.00	1.00	27.57	57.07
083	5.50	5.50	5.50	1.00	3.25	31.75	5.50	6.14	5.50	1.00	7.75	37.54	69.29
101							6.14	4.86	3.25	3.25	7.75	36.25	
102	4.86	6.14	5.50	3.25	3.25	34.00	4.86	6.14	5.50	3.25	3.25	34.00	68.00
108	4.86	6.79	5.50	3.25	3.25	35.29	4.86	5.82	5.50	3.25	3.25	33.36	68.64
113							4.86	4.21	5.50	1.00	3.25	27.89	
116	6.14	6.79	5.50	1.00	1.00	33.36	6.14	4.21	3.25	1.00	5.50	30.46	63.82
117	4.86	5.18	5.50	1.00	5.50	32.07	4.86	7.43	5.50	1.00	7.75	38.82	70.89
118	4.86	4.86	5.50	5.50	1.00	31.43	3.57	6.79	1.00	1.00	5.50	28.21	59.64

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
122	4.86	6.14	5.50	1.00	5.50	34.00	4.86	8.07	5.50	7.75	5.50	44.61	78.61
123							5.50	6.14	5.50	1.00	5.50	35.29	
125							4.86	4.86	5.50	1.00	5.50	31.43	
202	5.50	6.14	5.50	1.00	5.50	35.29	5.50	8.07	5.50	1.00	5.50	39.14	74.43
203	6.14	6.14	1.00	1.00	3.25	29.82	6.14	4.21	1.00	1.00	3.25	25.96	55.79
204	4.86	6.14	5.50	1.00	5.50	34.00	6.14	7.11	1.00	1.00	1.00	29.50	63.50
208	6.14	5.50	10.00	7.75	1.00	42.04	6.14	6.14	10.00	1.00	1.00	36.57	78.61
209	4.86	3.89	5.50	1.00	1.00	25.00	4.86	4.86	1.00	3.25	1.00	24.68	49.68
210	6.14	6.79	5.50	1.00	3.25	35.61	5.50	6.14	5.50	1.00	7.75	37.54	73.14
211	4.86	5.18	5.50	1.00	3.25	29.82	4.86	6.79	5.50	1.00	3.25	33.04	62.86
213							6.79	6.46	5.50	10.00	10.00	52.00	
215	6.14	5.18	5.50	1.00	5.50	34.64	6.14	7.43	1.00	1.00	3.25	32.39	67.04
217	4.86	5.50	5.50	1.00	3.25	30.46	4.86	6.14	1.00	1.00	7.75	31.75	62.21
218							4.86	6.14	1.00	1.00	3.25	27.25	
219							6.79	6.79	5.50	1.00	5.50	39.14	
224	6.14	6.79	7.75	3.25	5.50	42.36	6.14	7.43	5.50	1.00	7.75	41.39	83.75
226	6.79	4.21	5.50	3.25	5.50	36.25	4.86	3.89	5.50	3.25	1.00	27.25	63.50
227	7.43	7.43	5.50	3.25	1.00	39.46							
228	4.86	6.14	5.50	1.00	1.00	29.50	4.86	7.43	5.50	1.00	5.50	36.57	66.07
301	4.86	6.14	7.75	1.00	1.00	31.75	6.14	6.46	3.25	1.00	5.50	34.96	66.71
302	6.14	7.43	5.50	3.25	7.75	43.64	4.86	2.29	5.50	1.00	5.50	26.29	69.93
304	5.50	6.14	1.00	5.50	5.50	35.29	6.14	6.14	5.50	3.25	3.25	36.57	71.86
305	4.86	6.14	5.50	5.50	1.00	34.00	4.86	6.79	3.25	3.25	5.50	35.29	69.29
306	6.14	7.43	5.50	5.50	7.75	45.89	4.86	6.79	5.50	3.25	5.50	37.54	83.43
307	6.14	5.50	5.50	1.00	5.50	35.29	7.43	6.79	5.50	3.25	5.50	42.68	77.96

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
308	4.86	6.79	5.50	1.00	5.50	35.29	4.86	6.14	5.50	1.00	5.50	34.00	69.29
309	4.86	6.14	5.50	1.00	1.00	29.50	4.86	6.79	7.75	3.25	3.25	37.54	67.04
310	5.50	2.93	5.50	3.25	5.50	31.11	6.14	7.43	5.50	3.25	5.50	41.39	72.50
311	4.86	7.43	5.50	5.50	7.75	43.32	4.86	5.50	1.00	1.00	5.50	28.21	71.54
312	4.86	4.21	5.50	1.00	1.00	25.64	3.57	4.21	5.50	1.00	10.00	32.07	57.71
313	6.14	4.54	5.50	1.00	1.00	28.86	3.57	4.21	5.50	1.00	1.00	23.07	51.93
314	4.86	4.86	5.50	1.00	5.50	31.43	4.86	3.57	5.50	1.00	5.50	28.86	60.29
315	4.86	5.50	5.50	1.00	1.00	28.21	6.14	4.21	5.50	1.00	5.50	32.71	60.93
316							4.86	4.86	1.00	3.25	3.25	26.93	
317							4.86	6.79	1.00	3.25	5.50	33.04	
318	4.86	6.46	3.25	1.00	1.00	27.89	4.86	7.43	1.00	1.00	10.00	36.57	64.46
321	6.14	9.36	7.75	10.00	1.00	49.75	7.43	10.00	10.00	10.00	5.50	60.36	110.11
324	4.86	4.21	5.50	1.00	1.00	25.64	4.86	3.57	5.50	1.00	5.50	28.86	54.50
325	5.50	4.21	5.50	3.25	10.00	38.18	5.50	4.86	5.50	1.00	5.50	32.71	70.89
326	6.14	4.86	5.50	1.00	1.00	29.50							
328	4.86	5.50	5.50	5.50	1.00	32.71	4.21	4.54	5.50	3.25	5.50	31.75	64.46
329	6.14	7.43	3.25	3.25	3.25	36.89	4.86	3.57	3.25	1.00	5.50	26.61	63.50
330	4.86	4.21	3.25	1.00	1.00	23.39	6.14	6.79	3.25	1.00	3.25	33.36	56.75
331	4.86	3.57	5.50	1.00	5.50	28.86	4.86	2.93	5.50	1.00	1.00	23.07	51.93
332	4.86		1.00	1.00	5.50	22.43	4.86	3.89	1.00	1.00	5.50	25.00	47.43
334	4.86	4.21	5.50	1.00	3.25	27.89	4.86	4.86	5.50	3.25	7.75	35.93	63.82
335	4.86	3.57	1.00	1.00	5.50	24.36	4.86	4.54	5.50	1.00	3.25	28.54	52.89
336	6.14	6.46	7.75	1.00	1.00	34.96	6.14	5.82	5.50	1.00	7.75	38.18	73.14
337	3.57	4.21	5.50	1.00	5.50	27.57	4.86	3.57	5.50	1.00	10.00	33.36	60.93
338	4.86	5.50	5.50	3.25	1.00	30.46	4.86	4.86	5.50	1.00	5.50	31.43	61.89

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
339	4.86	3.57	1.00	1.00	10.00	28.86	4.86	6.14	1.00	1.00	5.50	29.50	58.36
340	6.14	6.79	10.00	1.00	5.50	42.36	4.86	4.54	3.25	1.00	5.50	28.54	70.89
341	6.14	4.86	1.00	1.00	5.50	29.50	4.86	4.86	5.50	1.00	5.50	31.43	60.93
342	4.86	5.50	5.50	1.00	5.50	32.71	4.86	6.14	7.75	7.75	3.25	40.75	73.46
343	6.14	6.79	5.50	1.00	5.50	37.86	6.14	4.86	1.00	1.00	3.25	27.25	65.11
344							6.14	4.21	5.50	3.25	5.50	34.96	
345	4.86	6.79	1.00	1.00	1.00	26.29	5.50	4.86	7.75	1.00	5.50	34.96	61.25
346	4.86	2.29	5.50	1.00	5.50	26.29	6.14	4.21	1.00	1.00	7.75	30.46	56.75
347	4.86	5.50	5.50	5.50	1.00	32.71	6.14	7.43	3.25	1.00	5.50	36.89	69.61
348	4.86	4.21	5.50	1.00	5.50	30.14	7.43	10.00	5.50	5.50	5.50	51.36	81.50
349	4.86	3.25	5.50	1.00	5.50	28.21	4.86	3.57	5.50	1.00	5.50	28.86	57.07
350	4.86	6.14	5.50	3.25	5.50	36.25	4.86	7.43	5.50	1.00	3.25	34.32	70.57
352	6.14	5.50	5.50	3.25	3.25	35.29	4.86	5.50	5.50	3.25	1.00	30.46	65.75
353	6.14	6.14	5.50	1.00	1.00	32.07	3.57	4.86	5.50	1.00	1.00	24.36	56.43
356	5.50	4.86	5.50	1.00	5.50	32.71	4.21	3.57	1.00	1.00	3.25	20.82	53.54
357	4.86	4.21	5.50	1.00	1.00	25.64	4.86	4.86	5.50	3.25	1.00	29.18	54.82
358	4.21	4.86	5.50	3.25	1.00	27.89	3.57	4.86	1.00	1.00	10.00	28.86	56.75
359	7.43	8.71	10.00	10.00	3.25	55.54	4.21	4.21	5.50	3.25	3.25	28.86	84.39
361	4.86	4.21	5.50	1.00	5.50	30.14	6.14	9.36	5.50	1.00	10.00	47.50	77.64
362	4.86	5.82	3.25	3.25	5.50	33.36	4.86	4.86	5.50	3.25	7.75	35.93	69.29
363	4.86	5.82	5.50	7.75	5.50	40.11	4.86	4.86	5.50	1.00	5.50	31.43	71.54
364							5.50	4.54	5.50	1.00	1.00	27.57	
367	6.14	8.71	7.75	7.75	5.50	50.71	6.14	6.14	1.00	1.00	1.00	27.57	78.29
368							4.86	5.50	5.50	1.00	10.00	37.21	
369	6.14	6.46	5.50	5.50	3.25	39.46	5.50	4.54	1.00	1.00	5.50	27.57	67.04

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
370	4.86	4.54	1.00	3.25	3.25	26.29	6.14	6.14	3.25	1.00	3.25	32.07	58.36
371	4.86	6.79	5.50	1.00	1.00	30.79							
372							6.14	7.11	5.50	3.25	7.75	43.00	
375							6.14	7.11	1.00	1.00	1.00	29.50	
376	4.86	6.14	7.75	1.00	5.50	36.25							
379	6.14	7.11	5.50	1.00	7.75	40.75	6.14	5.82	1.00	1.00	7.75	33.68	74.43
401	4.86	5.50	5.50	1.00	3.25	30.46	4.86	6.79	1.00	1.00	1.00	26.29	56.75
402	7.43	9.36	5.50	10.00	1.00	50.07	3.57	6.79	5.50	5.50	5.50	37.21	87.29
404	4.86	5.50	5.50	1.00	1.00	28.21	6.14	6.14	5.50	3.25	3.25	36.57	64.79
405	5.50	6.14	7.75	10.00	1.00	42.04	6.14	6.79	1.00	1.00	5.50	33.36	75.39
406	4.86	4.21	1.00	1.00	5.50	25.64							
409	4.86	5.18	5.50	1.00	5.50	32.07	3.57	3.89	3.25	3.25	5.50	26.93	59.00
410	4.86	6.14	3.25	1.00	5.50	31.75	4.21	3.57	1.00	1.00	7.75	25.32	57.07
411	5.50	6.46	1.00	1.00	3.25	29.18	4.86	6.14	3.25	3.25	1.00	29.50	58.68
412	6.14	4.21	5.50	1.00	3.25	30.46	6.79	5.50	5.50	1.00	10.00	41.07	71.54
413	5.50	6.79	1.00	3.25	3.25	32.07	4.21	5.50	3.25	5.50	5.50	33.68	65.75
414	8.07	10.00	10.00	10.00	5.50	61.64	9.36	10.00	10.00	10.00	7.75	66.46	128.11
415	6.14	6.79	5.50	5.50	1.00	37.86	6.14	5.18	5.50	1.00	7.75	36.89	74.75
417	4.86	4.21	5.50	3.25	3.25	30.14	4.86	6.79	1.00	1.00	5.50	30.79	60.93
418							4.86	5.82	3.25	1.00	1.00	26.61	
420	6.79	7.43	3.25	5.50	5.50	42.68	6.14	6.79	3.25	1.00	5.50	35.61	78.29
421	4.86	4.54	5.50	3.25	1.00	28.54	5.50	4.86	5.50	1.00	5.50	32.71	61.25
422	5.50	6.14	5.50	3.25	3.25	35.29	4.86	4.86	3.25	1.00	1.00	24.68	59.96
423	5.50	8.07	5.50	3.25	3.25	39.14							
424	4.86	4.86	5.50	3.25	3.25	31.43	4.86	6.79	5.50	7.75	3.25	39.79	71.21

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
425							6.14	5.50	5.50	1.00	5.50	35.29	
428	6.14	6.14	5.50	1.00	3.25	34.32	4.86	7.43	1.00	1.00	5.50	32.07	66.39
429	6.14	9.36	1.00	10.00	3.25	45.25	4.86	7.43	3.25	1.00	1.00	29.82	75.07
430							5.50	6.46	5.50	5.50	5.50	40.43	
432	4.86	5.50	5.50	1.00	3.25	30.46	5.50	6.14	10.00	5.50	7.75	46.54	77.00
433							6.14	7.11	5.50	1.00	5.50	38.50	
434	4.86	6.14	5.50	1.00	3.25	31.75	4.86	7.43	5.50	1.00	5.50	36.57	68.32
436	4.86	4.86	1.00	1.00	1.00	22.43	6.14	7.43	5.50	1.00	3.25	36.89	59.32
439	4.86	6.14	5.50	1.00	3.25	31.75							
440	4.86	4.21	5.50	1.00	1.00	25.64	6.14	6.14	5.50	1.00	1.00	32.07	57.71
441	5.50	6.14	3.25	1.00	1.00	28.54	4.86	5.82	1.00	1.00	7.75	31.11	59.64
442							6.14	6.46	1.00	1.00	5.50	32.71	
443	4.21	5.50	5.50	3.25	5.50	33.68	4.86	7.43	1.00	1.00	7.75	34.32	68.00
444	4.86	6.14	1.00	3.25	7.75	34.00	4.21	6.46	5.50	3.25	7.75	37.86	71.86
445							4.86	4.86	5.50	1.00	3.25	29.18	
447							4.86	5.50	1.00	1.00	5.50	28.21	
448	4.86	6.14	5.50	1.00	7.75	36.25	4.86	5.18	5.50	1.00	5.50	32.07	68.32
450	7.43	8.07	10.00	10.00	7.75	58.75	4.86	6.14	3.25	1.00	3.25	29.50	88.25
451	7.43	9.36	5.50	1.00	1.00	41.07	4.86	3.89	5.50	1.00	5.50	29.50	70.57
453							4.86	6.79	5.50	1.00	5.50	35.29	
455	6.14	6.79	1.00	3.25	1.00	31.11							
456	4.86	4.21	5.50	1.00	1.00	25.64							
458							6.14	6.79	1.00	1.00	1.00	28.86	
459	6.14	4.86	1.00	1.00	5.50	29.50	6.14	8.71	1.00	1.00	3.25	34.96	64.46
501	4.86	7.43	1.00	3.25	1.00	29.82	4.86	6.79	1.00	1.00	1.00	26.29	56.11

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
502	4.86	7.43	5.50	1.00	3.25	34.32	4.86	7.43	1.00	1.00	7.75	34.32	68.64
503	4.86	6.79	5.50	5.50	1.00	35.29	4.86	7.43	5.50	5.50	3.25	38.82	74.11
505	3.57	4.86	5.50	1.00	1.00	24.36	4.86	6.14	5.50	1.00	3.25	31.75	56.11
506	4.86	6.79	3.25	1.00	3.25	30.79	6.14	7.43	1.00	1.00	3.25	32.39	63.18
507	4.86	6.79	5.50	1.00	1.00	30.79							
509	4.86	6.14	5.50	1.00	1.00	29.50	4.86	7.43	7.75	1.00	1.00	34.32	63.82
510							4.86	7.43	5.50	1.00	5.50	36.57	
515	6.14	9.36	10.00	10.00	3.25	54.25	6.79	9.36	10.00	10.00	5.50	57.79	112.04
516	4.86	6.79	5.50	3.25	5.50	37.54	4.86	6.79	1.00	1.00	1.00	26.29	63.82
517	3.57	6.14	10.00	1.00	1.00	31.43	6.14	6.79	5.50	1.00	5.50	37.86	69.29
518	4.86	6.14	7.75	1.00	5.50	36.25	3.57	6.79	3.25	1.00	5.50	30.46	66.71
519							4.86	6.79	3.25	1.00	5.50	33.04	
520	4.86	6.14	5.50	5.50	1.00	34.00	4.86	6.79	1.00	1.00	5.50	30.79	64.79
521	4.86	6.79	3.25	3.25	1.00	30.79	4.86	7.43	1.00	1.00	3.25	29.82	60.61
524	4.86	8.07	5.50	3.25	3.25	37.86							
525	6.14	6.79	1.00	1.00	3.25	31.11							
527	4.21	4.86	5.50	1.00	3.25	27.89	4.86	4.86	1.00	1.00	7.75	29.18	57.07
528	4.86	6.14	5.50	1.00	5.50	34.00	4.86	6.79	1.00	1.00	5.50	30.79	64.79
529	4.86	8.07	5.50	1.00	5.50	37.86	4.86	6.79	5.50	1.00	5.50	35.29	73.14
530							6.14	7.43	5.50	5.50	7.75	45.89	
532							4.86	6.79	1.00	1.00	5.50	30.79	
533							4.86	6.14	5.50	1.00	5.50	34.00	
535	4.86	6.79	1.00	1.00	3.25	28.54	6.14	7.43	5.50	3.25	5.50	41.39	69.93
536	6.14	3.57	5.50	1.00	1.00	26.93	6.14	5.82	5.50	3.25	1.00	33.68	60.61
601	4.86	3.57	5.50	1.00	1.00	24.36	3.57	5.50	5.50	1.00	3.25	27.89	52.25

Table 16—Continued.

Nest	Male						Female						Pair Hybrid Index
	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	Back	Wingtips	Beak	Orbital Ring	Iris	Hybrid Index	
602	6.14	6.79	5.50	1.00	3.25	35.61	4.86	3.57	5.50	3.25	5.50	31.11	66.71
603	3.57	3.89	1.00	1.00	3.25	20.18	4.86	4.86	1.00	1.00	10.00	31.43	51.61
604	6.14	4.21	5.50	10.00	5.50	41.71	4.86	6.79	5.50	5.50	5.50	39.79	81.50
605	4.86	4.21	5.50	1.00	3.25	27.89	6.14	5.82	7.75	1.00	3.25	35.93	63.82
606	6.14	6.79	7.75	3.25	3.25	40.11	3.57	2.93	5.50	1.00	5.50	25.00	65.11
607	4.86	2.93	5.50	1.00	1.00	23.07	4.86	3.57	1.00	1.00	5.50	24.36	47.43
608	4.86	6.79	5.50	7.75	10.00	46.54	4.86	4.54	5.50	1.00	3.25	28.54	75.07
609							6.14	6.79	5.50	1.00	10.00	42.36	
611	4.86	3.57	5.50	5.50	3.25	31.11	3.57	2.93	5.50	1.00	5.50	25.00	56.11
612	4.86	4.86	1.00	3.25	5.50	29.18	4.86	5.50	5.50	3.25	3.25	32.71	61.89
613							3.57	2.93	5.50	5.50	3.25	27.25	
614	5.50	5.50	5.50	1.00	3.25	31.75	3.57	3.25	5.50	1.00	5.50	25.64	57.39
615	4.21	2.93	5.50	1.00	1.00	21.79	4.21	2.93	10.00	1.00	5.50	30.79	52.57
616	4.86	5.50	7.75	10.00	7.75	46.21	5.50	4.21	5.50	1.00	5.50	31.43	77.64
617	4.86	6.46	7.75	3.25	5.50	39.14	3.57	4.21	3.25	1.00	1.00	20.82	59.96
618	6.14	4.54	5.50	5.50	1.00	33.36	6.14	6.79	5.50	1.00	1.00	33.36	66.71
619	4.86	4.21	5.50	1.00	3.25	27.89	4.86	4.54	5.50	1.00	1.00	26.29	54.18
620	4.86	6.14	5.50	3.25	5.50	36.25	4.86	4.86	1.00	1.00	7.75	29.18	65.43
621	4.86	4.21	5.50	3.25	5.50	32.39	4.86	5.50	5.50	5.50	5.50	37.21	69.61
622	4.86	5.82	1.00	3.25	1.00	26.61	4.86	6.14	3.25	1.00	10.00	36.25	62.86
623	6.14	6.14	5.50	5.50	3.25	38.82	6.14	5.82	3.25	3.25	5.50	35.93	74.75
624	5.50	4.21	5.50	3.25	5.50	33.68	6.14	4.86	1.00	1.00	3.25	27.25	60.93
625	4.86	4.21	5.50	1.00	3.25	27.89	4.86	4.21	5.50	1.00	5.50	30.14	58.04
626	4.86	5.50	5.50	7.75	1.00	34.96	6.14	7.11	3.25	3.25	1.00	34.00	68.96
627	4.86	6.14	5.50	3.25	1.00	31.75	3.57	3.57	5.50	1.00	5.50	26.29	58.04

Table 17. Nest habitats and reproductive success.

Nest	Habitat	Clutch Size	Number of Successful Eggs	Number of Unfinished Eggs	A Egg Mass (g)	B Egg Mass (g)	C Egg Mass (g)
1	BS	3	3	0	92.9 ^a	87.9 ^a	88.3
4	BS	3	1	0	96.6	95.4	91.4
5	BS	3	3	0	93.9	101.9	94.9
10	BS	3	1	0	92.6	93.6	89.8
12	BS	4	2	0	98.1	100.9	99.8
13	BS	3	2	0	104.1	103.5	99.4
22	SV	2	1	0	92.9	86.1	
24	BS	3	2	0	105.0	103.4	96.1
26	SV	2	0	0	93.1	88.9	
27	BS	3	2	0	93.9	91.9	87.0
28	SV	3	3	0	100.4	98.9	90.3
33	BS	3	0	0	104.0	97.8	93.8
34	SV	3	2	0	89.2	85.5	84.0
35	BS	3	2	0	86.5	93.8	91.1
37	SV	3	3	0	87.8	89.1	83.2
41	BS	2 ^b	2 ^c	0	98.6	91.6	
42	SV	2	0	0	91.4	89.5	
43	BS	3	3	0	99.8	98.5	88.9
44	SV	3	2	0	91.9	97.4	91.6
45	BS	3	0	0	109.2	94.4	89.8
47	BS	3	3	0	102.3	101.2	90.5
48	BS	3	3	0	92.2	97.0	91.9
49	BS	3	3	0	91.5	93.6	81.6
50	BS	3	2	0	91.0	88.2	85.0
52	BS	3	3	0	103.5	99.4	99.1
53	SV	2	0	0	95.4	76.0	
54	BS	2	1	0	107.4	91.7	
55	BS	3	2	0	84.1	86.0	79.4
57	CN	3	1	0	109.1	107.9	99.8
58	LN	3	2	0	90.5	88.3	83.2
60	SV	3	2 ^c	0	97.4	98.4	94.9
61	BS	3	1	1	96.4	96.7	93.7
63	SV	2	0	0	98.1	98.0	
64	SV	3	0	2	98.5	98.0	93.8
66	BS	3	0	2	98.6	104.4	100.9
67	SV	1	0	1	107.7		
68	BS	3	0	2	97.0	96.8	80.8
69	SV	2	0	0	76.8	72.0	
73	SV	2	0	0	97.1	98.7	
75	BS	2	0	0	95.9	100.1	d

Table 17—Continued.

Nest	Habitat	Clutch Size	Number of Successful Eggs	Number of Unfinished Eggs	A Egg Mass (g)	B Egg Mass (g)	C Egg Mass (g)
77	LN	2	0	1	84.4	84.4	
78	SV	2	0	0	95.3	92.7	
83	BS	3	0	3	98.6	98.3	85.4
101	TT	3	3	0	105.6 ^a	107.3 ^a	100.6
102	BS	3	3	0	91.6	90.7	85.6
108	TT	3	3	0	108.1	108.2	99.4
113	BS	3	3	0	102.2	95.4	89.1
116	TT	3	3	0	90.9	89.2	83.1
117	TT	2	2	0	88.5	91.8	
118	LN	3	3	0	88.7	89.5	89.6
122	LN	3	3	0	91.4	90.4	83.6
123	TE	3	3	0	115.2	110.5	102.5
125	LN	3	1	2	103.5	100.1	88.1
202	TT	3	3	0	95.4	94.9	90.7
203	TE	3	3	0	98.6	97.8	89.7
204	BS	3	3	0	94.3	100.3	92.2
208	BS	3	1	0	88.2	88.4	78.5
209	BS	2	1	0	90.4	87.5	
210	TT	3	3	0	90.8	84.1	81.3
211	TT	2	1	0	108.9	104.8	
213	TT	3	3	0	95.2	92.1	85.9
215	SV	3	2	0	95.1	88.7	86.3
217	SV	3	3	0	100.4	103.5	97.3
218	BS	3	3	0	88.9 ^a	83 ^a	80.0
219	BS	2	2	0	95.6	97.9	
224	TE	2 ^b	1 ^c	0	105.9	99.5	
226	TE	3	2	1	90.4	89.2	88.0
227	BS	1	1	0	85.8		
228	TT	3	1	0	98.6	97.3	90.1
301	CC	3	2	0	79.3	79.7	74.1
302	BS	3	2	0	86.0 ^a	91.0 ^a	90.4
304	BS	3	3	0	100.4	100.7	95.2
305	LB	3	3	0	95.6	101.2	95.5
306	CC	2	2	0	93.4	89.1	
307	CC	3	3	0	94.8	91.6	83.0
308	LN	3	3	0	91.4	90.2	85.9
309	LB	3	0	0	101.8	95.3	89.1
310	BS	3	2	0	96.0	92.3	89.8
311	BS	3	3	0	91.7	94.0	84.5
312	LB	3	3	0	91.2	90.5	85.0

Table 17—Continued.

Nest	Habitat	Clutch Size	Number of Successful Eggs	Number of Unfinished Eggs	A Egg Mass (g)	B Egg Mass (g)	C Egg Mass (g)
313	SV	3	2	0	102.8	105.3	98.8
314	BS	3	2	0	103.0	105.8	95.1
315	CC	3	3	0	103.5	98.2	95.3
316	CC	3	0	0	102.9	97.9	92.1
317	SV	3	3	0	100.8	97.0	91.5
318	BS	2	2	0	85.6	84.6	
321	CC	3	3	0	96.6	96.9	83.9
324	BS	3	3	0	103.6	101.9	101.4
325	SV	3	2	0	99.0	94.6	93.6
326	LB	2	2	0	93.0	85.6	
328	CN	3	3	0	93.3	97.1	99.2
329	LB	3	3	0	101.2	102.4	97.8
330	BS	3	3	0	88.9	94.2	88.1
331	LB	2	2	0	96.4	89.1	
332	SV	2	1	0	85.8	82.8	
334	LB	3	0	0	108.4	97.2	92.7
335	BS	3	2	0	89.0	84.3	86.2
336	LB	3	3	0	90.2	89.4	82.2
337	SV	3	2	0	94.8	89.8	87.4
338	CC	3	3	0	113.5	110.9	105.7
339	SV	3	3	0	94.3	100.0	93.9
340	BS	3	3	0	102.8	101.9	98.3
341	BS	2	2	0	97.1	94.9	
342	BS	3	2	0	94.1	99.2	97.4
343	CC	3	2	0	76.8	81.1	77.6
344	LB	3	2	0	95.8	103.1	94.6
345	SV	3	3	0	95.3	90.9	86.7
346	SV	3	2	0	89.3	95.2	97.2
347	SV	2	2	0	92.1	85.8	
348	BS	3	2	0	94.4	100.2	94.7
349	CC	2	2	0	90.1	86.7	
350	CC	3	2	0	98.6	98.7	94.1
352	SV	3	2	0	101.7	99.1	98.9
353	LB	3	3	0	95.9	99.3	97.8
356	SV	3	3	0	101.7	101.4	100.7
357	SV	2	2	0	97.9	96.0	
358	LB	2	2	0	99.0	95.8	
359	BS	2	2	0	103.2	103.0	
361	CC	3	2	0	96.8	94.5	93.1
362	SV	3	3	0	95.2 ^a	95.1 ^a	91.3

Table 17—Continued.

Nest	Habitat	Clutch Size	Number of Successful Eggs	Number of Unfinished Eggs	A Egg Mass (g)	B Egg Mass (g)	C Egg Mass (g)
363	BS	3	2	1	103.8	106.5	96.7
364	SV	3 ^b	2 ^c	1	86.5	87.0	80.8
367	LB	3	0	0	93.5	92.9	88.3
368	BS	1	0	1	111.5		
369	SV	3	0	3	101.6	98.0	91.4
370	CC	3	0	3	97.2	91.7	86.7
371	BS	2	0	2	99.7	101.2	
372	CN	1	0	1	84.6		
375	BS	3	0	3	95.6	92.3	83.5
376	SV	3	0	3	95.3	94.7	86.6
379	LB	3	0	3	96.6	96.3	84.9
401	BS	6	3	0			
402	BS	3	3	0	90.5	89.1	87.2
404	CC	3	2	0	97.1	99.2	90.8
405	SV	4	2	0	101.4	98.7	101.2
406	BS	3	3	0	104.9	101.3	96.1
409	SV	3	1	0	81.5	81.2	81.2
410	BS	3	2	0	91.9	92.2	88.8
411	SV	3	2	0	100.1	104.0	102.9
412	BS	3	3	0	105.9	104.2	99.7
413	SV	3	2	0	106.8	109.9	95.7
414	BS	3	3	0	99.3	98.0	94.1
415	LN	3	3	0	99.8	101.5	92.1
417	BS	3	3	0	93.3	93.6	91.3
418	CN	3	2	0	92.1	90.5	91.0
420	SV	3	1	0	98.6	103.4	91.3
421	SV	3	3	0	88.8	93.0	94.9
422	BS	3	1	0	90.1	95.2	87.1
423	SV	2	1	0	100.8	103.5	
424	SV	3	2	0	103.0	101.2	92.1
425	BS	2	2	0	85.0	79.0	
428	SV	3	3	0	98.7	98.3	98.2
429	SV	2	1	0	83.5	80.9	
430	SV	3	1	0	96.4	95.9	89.9
432	BS	3	3	0	86.3	86.6	83.2
433	LB	2	2	0	98.1	96.7	
434	SV	3	1	0	93.4	96.0	93.2
436	SV	3	3	0	101.6	107.9	105.4
439	SV	3	2	0	94.7	95.5	91.3
440	BS	3	2	0	96.3	97.3	93.2

Table 17—Continued.

Nest	Habitat	Clutch Size	Number of Successful Eggs	Number of Unfinished Eggs	A Egg Mass (g)	B Egg Mass (g)	C Egg Mass (g)
441	BS	2	1	0	93.7	93.8	
442	SV	3	0	1	97.9	107.6	109.9
443	BS	2	1	0	92.7	87.1	
444	SV	2	1	0	88.7	90.6	
445	CC	2	0	0	112.2	95.5	
447	CN	2	1	0	98.4	97.9	
448	BS	3	2	1	78.4	81.0	71.8
450	BS	3	1	1	94.0	98.0	90.3
451	BS	2	0	1	92.1	92.7	
453	BS	3	0	2	98.4	105.5	99.1
455	BS	1	0	0	81.7		
456	BS	2	0	1	76.2	80.4	
458	CC	2	0	1	81.3	74.9	
459	SV	3	0	1	92.9	90.4	86.8
501	BS	3	1	0	92.9	84.7	82.5
502	BS	3	2	0	109.7	103.3	97.7
503	BS	3	2 ^c	0	99.7	98.1	95.7
505	BS	3	1	0	79.1	75.4	72.6
506	BS	3	3	0	100.2	98.5	94.8
507	BS	3	2	0	91.9	94.5	92.2
509	BS	3	2	0	106.1	103.4	101.0
510	SV	3	2	0	95.5	100.3	95.8
515	SV	3	2	0	89.3	87.1	81.1
516	BS	3	2	0	99.4	97.8	94.7
517	BS	3	2	0	92.9	97.1	88.4
518	SV	2	2	0	93.0	98.4	
519	LN	3	3	0	107.8	104.3	97.8
520	BS	3	3	0	109.4	110.8	102.5
521	SV	3	3	0	90.2	97.0	90.7
524	SV	2	2	0	92.4	88.8	
525	BS	3	3	0	92.9	84.4	85.2
527	BS	3	3	0	94.4	96.4	88.3
528	BS	3	3	0	90.1	89.8	87.6
529	SV	3	2	0	90.9	86.9	86.8
530	SV	2	2	0	104.9	93.3	
532	SV	3	0	2	91.8	86.1	79.6
533	SV	2	1	0	97.2	87.1	
535	SV	3	0	1	93.3	90.5	84.1
536	SV	3	0	1	87.9	89.4	82.3
601	LN	3	3	0	97.8	98.1	88.6

Table 17—*Continued.*

Nest	Habitat	Clutch Size	Number of Successful Eggs	Number of Unfinished Eggs	A Egg Mass (g)	B Egg Mass (g)	C Egg Mass (g)
602	SV	2	1	0	90.9	85.5	
603	CC	3	3	0	82.0	82.5	83.4
604	BS	3	3	0	102.8	104.8	97.6
605	SV	3	2	0	93.3	93.9	62.4
606	LB	3	3	0	89.7	91.6	86.2
607	SV	2	1	0	92.2	89.9	
608	BS	3	3	0	85.7	89.9	86.6
609	LB	4	2	0	105.0	95.4	89.8
611	CN	3	1	0	103.7	95.7	93.7
612	BS	2	2	0	88.5	93.7	
613	CN	3	1	0	99.2	97.3	93.4
614	LN	3	3	0	91.2	94.4	94.4
615	LN	3	2	0	110.8	115.6	107.1
616	LB	3	0	0	89.5	93.9	87.0
617	LB	3	2	0	99.8	102.0	99.8
618	CC	3	2	0	90.7	96.5	94.3
619	SV	3	2	0	113.8	106.7	98.7
620	SV	2	2	0	92.9	89.1	
621	LB	3	0	2	92.5	88.1	88.2
622	SV	2	2	0	92.3	84.3	
623	LN	3	3	0	90.7	80.8	78.5
624	CC	3	3	0	106.2	96.1	95.2
625	BS	3	1	2	119.6	114.8	110.3
626	SV	3	0	0	84.5	79.2	69.1
627	SV	2	0	2	79.5	80.8	

^a Egg could have been either the first or second egg of the clutch (“AB” or “BA” egg); this egg was left out of mass analyses.

^b Omitted from clutch size analyses due to ambiguity in or issues with clutch size.

^c Omitted from hatching success analyses due to ambiguity in number successful (e.g. I was unable to determine whether one chick hatched or was predated).

^d I failed to get the mass for this egg.

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