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Honors Thesis

Mating Patterns and Breeding Success in the *Larus glaucescens-occidentalis* Complex, Protection Island, Washington

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

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

Interspecific hybridization has been well documented among large white-headed gulls of the genus *Larus* (Pierotti 1987; Bell 1996; Howell and Dunn 2007). Members of this genus differ minimally in features such as size, back and wingtip melanism, and bare-part coloration, and this phenotypic similarity appears to facilitate hybridization (Hoffman and others 1978; Pierotti 1987). Interbreeding between Glaucous-winged Gulls (*Larus glaucescens*) and Western Gulls (*Larus occidentalis occidentalis*) in the Pacific Northwest has not been noted since the early 20th century (Dawson 1908). *L. glaucescens* is also known to hybridize with members of three other gull species in the North Pacific and Bering Sea region: Herring Gulls (*L. argentatus*; Williamson and Peyton 1963), Glaucous Gulls (*L. hyperboreus*; Strang 1977; McCaffery and others 1997), and Slaty-backed Gulls (*L. schistisagus*; Howell and Dunn 2007). In contrast, *L. occidentalis* is not known to hybridize with any species besides *L. glaucescens*. The presence of reproductively viable offspring from naturally occurring *L. glaucescens-occidentalis* hybrid pairs suggests that they represent a single species. However, factors such as the presence of assortative mating based on morphology and the limited size of the hybrid zone support the current classification of *L. glaucescens* and *L. occidentalis* as separate species (Hoffman and others 1978; Bell 1996; Good and others 2000).

The *L. glaucescens-occidentalis* hybrid zone occurs along a transition between two marine ecosystems, the first characterized by fjords and estuaries and the second by the California Current and coastal upwelling (Bell 1996). *L. glaucescens* breeds from western Alaska south along the Pacific Coast to northern Oregon and has adapted to the first ecosystem; by contrast, *L. occidentalis* breeds from northern Washington to Baja California and has adapted to the second ecosystem (Bell 1996; Howell and Dunn 2007).

In previous work, the relationship between the ecotone and the hybrid zone has been of particular interest, as it potentially explains why hybrids thrive in coastal Washington and Oregon (Bell 1996; Good and others 2000). Good and others (2000) argued that *L. glaucescens-occidentalis* hybrids outcompete parental species in the ecotone by combining the adaptive abilities of the parental species. They found, as did Hoffman (1978), that pairs with hybrid members had significantly greater reproductive success than pairs without a hybrid member. In contrast, Bell (1997) found that pairs with at least one *L. occidentalis* member experienced greater reproductive success than other pair combinations; Bell suggested that shifting conditions in the ecotone may favor hybrids some years and a parental species other years. Clearly, multiple factors determine reproductive success in the *L. glaucescens-occidentalis* complex.

I conducted a study on Protection Island National Wildlife Refuge, WA, which is located in the Salish Sea at the northern end of the *L. glaucescens-occidentali*s hybrid zone (Bell 1996). Previous studies of mating patterns and reproductive success in the *L. glaucescens-occidentalis* complex have been limited to sites on the outer coast (Hoffman and others 1978; Bell 1997; Good and others 2000). Previous investigation of the *L. glaucescens-occidentalis* complex on Protection Island has been limited to work by Bell (1996). He collected 17 gulls on Protection Island and determined their phenotypes; however, Bell did not measure the reproductive success of these birds. My work provides the first extensive phenotype description of the *L. glaucescens-occidentalis* complex on Protection Island, and the first assessment of breeding success of this complex in the Salish Sea. I tested the null hypotheses that no assortative mating occurred among the gulls, and that there was no relationship between reproductive success and phenotype.

METHODS

DEVELOPMENT OF THE HYBRID INDEX

To characterize gull phenotypes I used a hybrid index based on work by Bell (1996, 1997) designed specifically for members of the *L. glaucescens-occidentalis* complex. The index included ratings of 5 characters: wingtip and back (mantle plus scapulars) melanism and beak, orbital ring, and iris color (Table 1). Higher index values corresponded to more *L. occidentalis*-like phenotype. In contrast to several previous studies that used the Munsell 37-step neutral value scale, I quantified plumage melanism using the 19-step Kodak Gray Scale because of its accessibility, ease of use in the field, and application to gull plumage by Howell and Dunn (2007). Because methodologies described by previous investigators lack precise details in how to score plumage melanism with a gray scale, it could be misleading to compare results with those in previous studies, even if using the Munsell scale. The shades of the Kodak Gray Scale range from very pale gray (1) to black (19). Although the back and wingtips of adult gulls often show slight bluish or brownish tones, respectively, the shades can still be approximated with a neutral gray scale.

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

DATA COLLECTION

My study site was a breeding colony of gulls of the *L. glaucescens-occidentalis* complex located on Violet Point, Protection Island National Wildlife Refuge (UTM zone 10, 506039.29 m E, 5330576 m N), Jefferson County, WA. On 24, 25, 27, and 28 June 2010 two of us (AEM and Libby Megna) independently used the hybrid index to quantify phenotypes in a study area previously set up to monitor gull reproductive success. We worked when the sky was overcast, avoiding sunny and low angle light conditions, which can variably affect the appearance of plumage melanism through shadows, backlighting, or washing out of color (Howell and Dunn 2007). Average feather shade and bare-part coloration were determined at close quarters, mostly within 3 m, using naked eye observations useful for comparing individuals, binoculars, and a Nikon Fieldscope 82mm ED.

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

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

DATA SCALING AND ANALYSIS

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

For analyses of multiple characters, I summed the beak, orbital ring, and iris scores to generate the bare-part score, and I summed the back and wingtip scores to generate the back-wingtip score. I defined the overall hybrid index as the sum of the bare-part score and two times the back-wingtip score. The back-wingtip score was doubled because plumage melanism is considered the best way to visually distinguish hybrids from pure birds (Bell 1996).

I collected complete hybrid index data for 81 pairs. Pairs were selected on the basis of availability during data collection. The significance level chosen for statistical tests was 0.05. Using Pearson correlation analyses I tested the degree of assortative mating and the relationship between hybrid index and egg mass. The correlations between hybrid index and mass of the 3rd egg in the clutch were carried out for 49 of 81 pairs, because the remaining nests did not contain a 3rd egg. Phenotype differences between the 81 males and 81 females were analyzed using the Mann-Whitney U test. Using ordinal logistic regression (MATLAB 2011) I tested whether gulls with mid-range hybrid index values—hybrid-type gulls—had significantly greater clutch size or hatching success than birds with low or high hybrid index values—parental-type gulls. For this analysis I adjusted all hybrid index values to reflect their distance from the midpoint of the range of observed hybrid indices (40.75). Male and female hybrid indices were adjusted by taking their absolute difference from the midpoint, while pair indices were adjusted by taking their absolute difference from two times the midpoint. Thus, higher adjusted hybrid index values correspond to more parental-like phenotypes, whereas lower adjusted hybrid index values correspond to more hybrid-like phenotypes. Clutch size data were obtained and analyzed for 81 pairs, while egg fate data were obtained and analyzed for 69 pairs. I defined clutch size as the total number of eggs laid per nest and hatching success as the number of eggs hatched per nest.

RESULTS

The appearance of the gulls on the Violet Point colony tended towards the *L. glaucescens* phenotype, although a wide range of phenotypes were present (Fig. 1). Average female wingtip, iris, and hybrid index scores were significantly higher (indicating more like *L. occidentalis*) than corresponding male scores (Table 2). Male hybrid index and female hybrid index were significantly correlated (r = 0.44, df = 79, p = 0.00004; Fig. 2). However, when the 3 pairs with the highest hybrid indices were removed, the correlation was insignificant (r = 0.13, df = 76, p = 0.24). The correlation between male back-wingtip score and female back-wingtip score was also significant (r = 0.25, df = 79, p = 0.02).

Correlations between various phenotypic characters and the masses of the 1st and 2nd eggs in the clutch were not significant. However, male back-wingtip score was significantly indirectly correlated with the mass of the 3rd egg in the clutch (r = -0.31, df = 47, p = 0.03; Fig. 3). The correlation between the male hybrid index and the mass of the 3rd egg was not quite significant, although it showed the same trend (r = -0.28, df = 47, p = 0.05). No significance was found in the correlation between female back-wingtip score and the mass of the 3rd egg (r = 0.008, df = 47, p = 0.96), or between female hybrid index and the mass of the 3rd egg (r = -0.09, df = 47, p = 0.54). Ordinal logistic regression showed no significant difference in hatching success or clutch size between hybrid-type gulls and parental-type gulls (Table 3).

DISCUSSION

Protection Island is located towards the northern boundary of the hybrid zone (Bell 1996), so as expected the phenotypes on the Violet Point gull colony tended towards *L. glaucescens* (Fig. 1). The scarcity of *L. occidentalis*-type gulls on the colony was also noted by Bell (1996). After collecting 17 gulls from Protection Island he determined that 8 were *L. glaucescens*, 8 were hybrids, and 1 was *L. o. occidentalis*. I found that females appeared significantly more like *L. occidentalis* than males in terms wingtip, iris, and hybrid index scores (Table 2). The reason for these differences is entirely unknown, and I hesitate to assign them any biological significance.

I observed significant assortative mating by morphology across our sample of 81 gull pairs (Fig. 2); however, when I removed the 3 pairs with the highest hybrid indices from the analysis there was no significance. Thus, it appears that a few *L. occidentalis*-like gulls on the colony contributed most to the trend of assortative mating, while gulls of intermediate or *L. glaucescens*-like phenotype contributed very little. Both Bell (1997), and Hoffman and others (1978) also documented assortative mating based on colorimetric characters in the *L. glaucescens-occidentalis* complex. In contrast, Good and others (2000) found weak evidence of assortative mating on one colony and none on another colony. Although assortative mating is an indication of species divergence (Hoffman and others 1978), Good and others (2000) argue that absence of assortative mating does not necessarily indicate conspecificity, given that selection should preserve the parental species outside the hypothesized zone of hybrid superiority. Because significant assortative mating was found in 2 of 3 previous studies, I believe that assortative mating is the general mating pattern among the gulls in the hybrid zone. The evidence that hybrids are confined to the ecotone in coastal Washington and Oregon also enforces distinctness between the two parental species (Good and others 2000). In agreement with previous investigators I believe that *L. occidentalis* and *L. glaucescens* should continue to be considered separate species due to the general presence of assortative mating and bounded nature of the hybrid zone (Hoffman and others 1978; Bell 1996; Good 2000). If the hybrid zone expands well beyond coastal Washington and Oregon in the coming years, this view should be carefully reconsidered.

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

The correlation between male and female back-wingtip scores was significant, but, with the addition of the bare-part score for the hybrid index, the correlation was tighter. This may in part be an artifact of the limited number of possible bare-part scores. However I agree with Bell (1996) that they do improve the accuracy of this specific hybrid index.

Most gulls produce 3-egg clutches (Good and others 2000), and the mass of the 3rd egg in the clutch is known to be a good indicator of parent health and energy reserves (Bell 1997). The significant indirect correlation between male back-wingtip score and 3rd egg mass was an unexpected result. No previous study has shown a significant decrease in egg mass with more *L. occidentalis*-like phenotypes. The absence of a similar trend with the female back-wingtip score is noteworthy. Good and others (2000) found that since females receive much of their food from males during egg formation, and that adult feeding habits affect reproductive success, male fitness can strongly influence egg size. Although the smaller egg mass indicates that *L.*

occidentalis may have had poorer breeding success, I observed no significant difference between hybrid-type and parental-type gulls in clutch size or hatching success—both more direct measures of breeding success. Thus, hybrid superiority in the *Larus glaucescens-occidentalis* complex was apparently not present on Protection Island in 2010. However, my results do not necessarily contradict the application of the bounded hybrid superiority hypothesis to the *L. glaucescens-occidentalis* complex by Good and others (2000). They found strongest evidence of hybrid superiority in Gray's Harbor at the middle of the hybrid zone where hybrids would be expected to maximize traits of both parental species.

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

This project contributes the first extensive phenotypic description of a *L. glaucescens-occidentalis* gull colony in the Salish Sea. The finding that significant assortative mating according to colorimetric characters occurs on Protection Island, especially among *L. occidentalis*-like gulls, supports the current classification of *L. glaucescens* and *L. occidentalis* as separate species. Protection Island appears to be outside of the proposed zone of hybrid superiority (Good and others 2000) because hybrids did not show greater reproductive success than parental phenotypes on the island in 2010.

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FIGURE CAPTIONS

FIGURE 1. Distribution of hybrid indices for gulls on Violet Point, Protection Island (n = 162). Median = 29.5. Mean = 30.7. A greater hybrid index value indicates a more *L. occidentalis*-like appearance.

FIGURE 2. The correlation between male hybrid index and female hybrid index was significant (r = 0.44, p = 0.00004; n = 81 pairs).

FIGURE 3. The indirect correlation between male back-wingtip score and mass of the 3rd egg in the clutch was significant (r = -0.31, p = 0.03, n = 49).

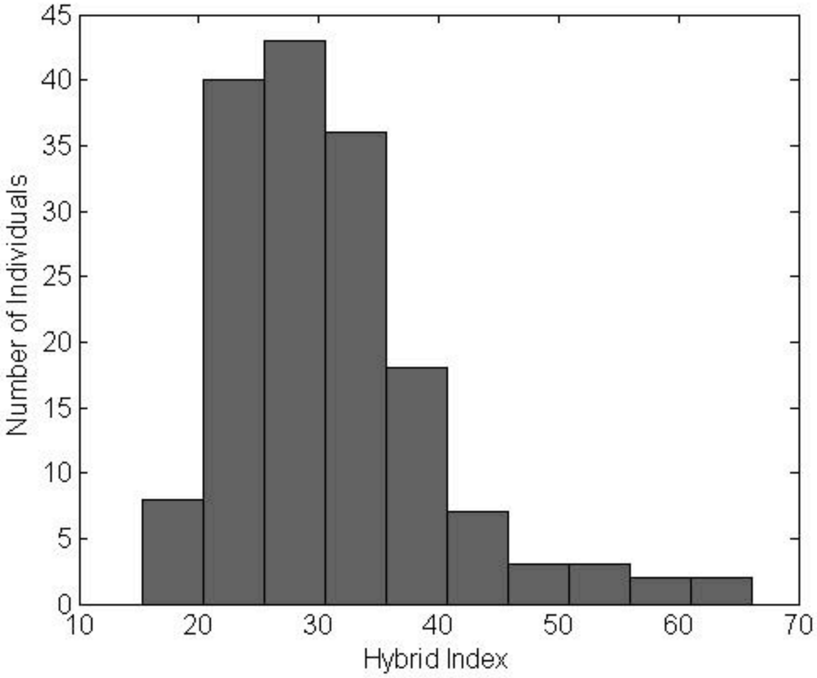
45
40
35
30
25
20
15
10
5
0
10
20
30
40
50
60
70
Number of Individuals
Hybrid Index

Figure 1

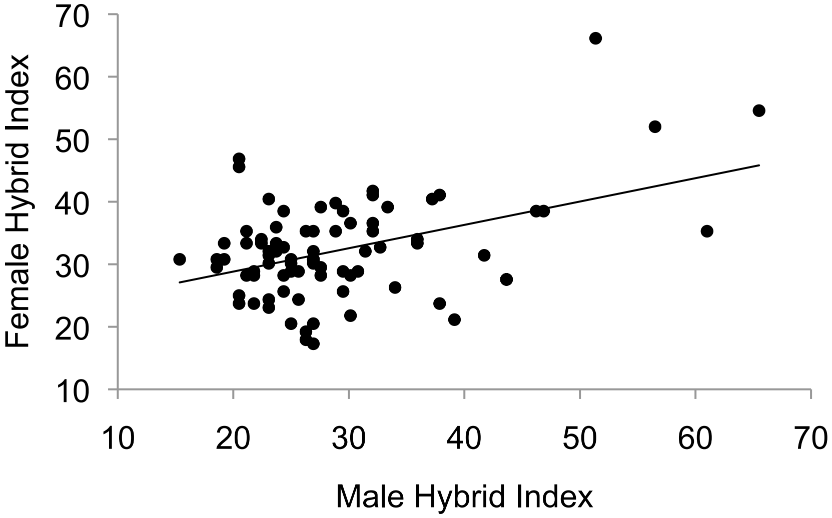
Female Hybrid Index
70
60
50
40
30
20
10
10
20
30
40
50
60
70
Male Hybrid Index

Figure 2

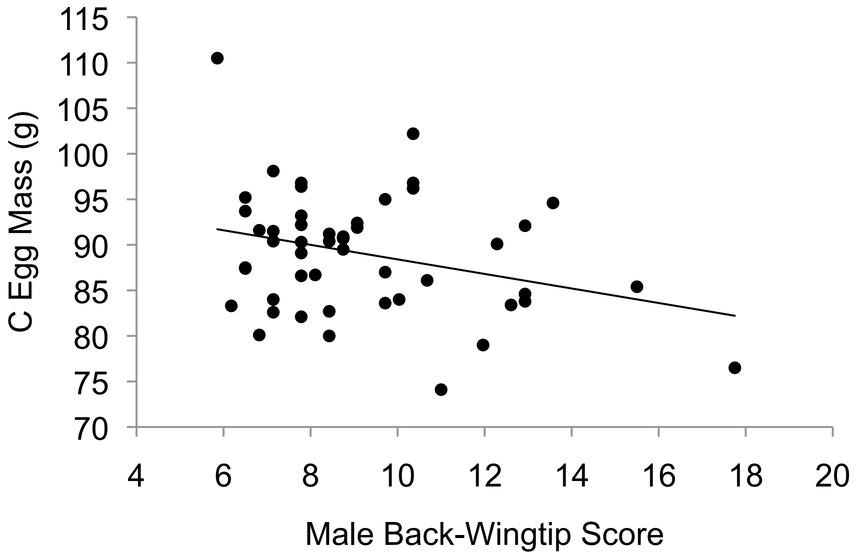
115
110
105
100
95
90
85
80
75
70
C Egg Mass (g)
4
6
8
10
12
14
16
18
20
Male Back-Wingtip Score

Figure 3

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

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

TABLE 2. Summary of male and female character scores (mean ± SD) and Mann-Whitney U tests (n = 81 pairs).

	Male	Female	U	p
Back	4.79 ± 1.17	5.00 ± 1.21	2883	0.17
Wingtips	4.27 ± 1.59	4.79 ± 1.85	2634	0.03
Beak	4.89 ± 2.44	4.78 ± 2.51	3206	0.76
Orbital ring	2.44 ± 2.83	2.17 ± 2.34	3206	0.73
Iris	3.72 ± 2.73	5.72 ± 2.84	2120	0.00001
Hybrid index	29.17 ± 9.48	32.25 ± 8.04	2233	0.0004

TABLE 3. Coefficients (β) and their standard errors (SE) and p-values, odds ratios (OR) and 95% confidence intervals for the ORs for ordinal logistic regression analysis of adjusted hybrid indices with clutch size and number hatched. For clutch size analyses, n = 81. For hatching success analyses, n = 69. The adjusted hybrid index (AHI) is the absolute difference between the hybrid index and the midpoint of the observed range of hybrid indices.

	B	SE[2]	p	c	OR[1]	95% CI	
Clutch size							
male AHI	-0.050	0.04	0.21	10	0.60	0.28	1.33
female AHI	-0.003	0.04	0.94	10	0.97	0.47	2.01
pair AHI	-0.022	0.02	0.35	20	0.64	0.25	1.64
Number hatched							
male AHI	-0.030	0.04	0.44	10	0.74	0.35	1.57
female AHI	0.043	0.04	0.24	10	1.54	0.75	3.14
pair AHI	-0.004	0.02	0.87	20	0.93	0.38	2.28

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

[2] Dispersion estimated.