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RESEARCH ARTICLE

Egg cannibalism in a gull colony increases with sea surface temperature

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ABSTRACT

Cannibalism occurs regularly across a broad range of taxa with a variety of ecological and evolutionary consequences. Rises in sea surface temperature (SST) have been linked to increased cannibalism in some species, including polar bears (*Ursus maritimus*), Peruvian anchovy (*Engraulis ringens*), and Peruvian hake (*Merluccius gayi peruanus*), and might be expected in birds that depend on marine food webs for sustenance. Increased SSTs are associated with lowered ocean thermoclines and weakened upwellings. These changes, in turn, lead to decreased productivity in surface water and movement of surviving forage fish to deeper water, thereby food-stressing surface feeders such as gulls, diminishing energy intake and lengthening foraging bouts. While controlling for a suite of other environmental factors, we tested whether egg cannibalism and hatching success were independent of rises in local SST at a colony of Glaucous-winged Gulls (*Larus glaucescens*) and Glaucous-winged × Western Gull (*L. glaucescens × occidentalis*) hybrids during 2006–2011 on Protection Island, Washington, USA. Cannibalism increased and hatching success decreased with rises in SST. It is unclear if rises in SST impact overall population trends. Gulls are multiyear breeders; if they experience reproductive failure during one or several El Niño-Southern Oscillation–related events, they typically have other opportunities to breed. With rising SSTs associated with climate change, however, increasing levels of cannibalism could lead to declining populations in the absence of compensatory adaptive modifications or range shifts.

Keywords: egg cannibalism, climate change, ENSO, Glaucous-winged Gull, *Larus glaucescens*, *Larus occidentalis*, sea surface temperature, Western Gull

El canibalismo de huevos en colonias de gaviotas aumenta con la temperatura superficial del mar

RESUMEN

El canibalismo ocurre regularmente en una amplia gama de grupos taxonómicos con una variedad de consecuencias ecológicas y evolutivas. El aumento de la temperatura superficial del mar (SST) se han relacionado con el aumento del canibalismo en algunas especies, como los osos polares (*Ursus maritimus*), la anchoveta peruana (*Engraulis ringens*) y la merluza peruana (*Merluccius gayi peruanus*), y podría esperarse en aves que dependen de las redes alimenticias marinas para su sustento. Aumentos de SST están asociados con termoclinas oceánicas más bajas y afloramientos debilitados. Estos cambios a su vez, conllevan a la disminución de la productividad en aguas superficiales y al movimiento de los peces que sirven como presa a aguas más profundas, lo que genera que especies como las gaviotas que se alimentan en la superficie sufran estrés, alargando sus periodos de forrajeo y disminuyendo su ingesta energética. Tras contralar una serie de factores ambientales, probamos si el canibalismo de huevos y el éxito de eclosión fueron independientes a los aumentos en SST locales en una colonia de *Larus glaucescens* e híbridos de *L. glaucescens* x *occidentalis* durante 2006–2011 en Protection Island, Washington. Con el de aumento de SST el canibalismo aumentó y el éxito de eclosión disminuyó. No es claro si el aumento en SST tiene un impacto en las tendencias generales de la población. Las gaviotas se reproducen durante múltiples años; así que si experimentan problemas reproductivos durante uno o varios eventos relacionados a El Niño–Oscilación del Sur, pueden tener otras oportunidades para reproducirse. Sin embargo, con el aumento de las SST asociadas al cambio climático, un aumento en los niveles de canibalismo, podría conducir a un decrecimiento de las poblaciones en ausencia de modificaciones adaptativas compensatorias o cambios de distribución.

Palabras clave: el canibalismo de huevos, cambio climático, ENSO, *Larus glaucescens*, *Larus occidentalis*, la temperatura superficial del mar

INTRODUCTION

Cannibalism, eating another individual of the same species, occurs regularly across a broad range of taxa, including protozoans, planaria, rotifers, platyhelminths, aschelminths, snails, copepods, centipedes, mites, insects, ascidians, fish, amphibians, reptiles, birds, and mammals (Fox 1975, Elgar and Crespi 1992). Cannibalism occurs among both carnivores and otherwise herbivorous animals such as leaf- and bark-eating insects (Kirkpatrick 1957, Brower 1961, Bygott 1972, Eickwort 1973, Beaver 1974, Hamai et al. 1992, Hiraiwa-Hasegawa 1992, Watts and Mitani 2000). Fox (1975) considered cannibalism a normal characteristic of many populations, and Polis (1981) found this behavior documented for some 1,300 species.

Cannibalism has a variety of ecological and evolutionary consequences. For example, it can influence population size, complicate energetic relationships in ecological communities, engender complex nonlinear population dynamics such as chaos, lower reproductive success, shape social behavior, and promote development of kin selection (Polis 1981, Elgar and Crespi 1992, Stanback and Koenig 1992, Cushing et al. 2002). Among colonial-nesting gulls, egg and chick cannibalism occur during intense agonistic territorial interactions (Tinbergen 1961, Hayward et al. 1977), and these events can result in substantial decreases in reproductive success (Gillett et al. 1975, Davis and Dunn 1976, Brouwer and Spaans 1994).

Numerous factors play a role in the occurrence of cannibalism. Fox (1975) listed crowding, peculiar behavior patterns by vulnerable individuals, physiological and psychological stress, and victim availability as important enabling factors. Genetics may play a role, with some individuals more prone than others to feed on conspecifics (Fox 1975, Polis 1981). Additional factors include size, age, developmental stage, sex, and habitat (Polis 1981, Baur and Baur 1986). The most common factors associated with cannibalism, however, are those associated with lack of food or poor food quality (Dong and Polis 1992). For example, melting sea ice and concomitant foraging habitat loss due to global warming may be responsible for cannibalism in polar bears (*Ursus maritimus*; Dyck and Daley 2002, Amstrup et al. 2006). El Niño–Southern Oscillation (ENSO) events leading to prolonged increases in sea surface temperature (SST) dramatically alter marine food webs and trophic relationships, including increased cannibalism of eggs and larvae by Peruvian anchovy (*Engraulis ringens*; Alheit and Niquen 2004) and Peruvian hake (*Merluccius gayi peruanus*; Guevara-Carrasco and Lleonart 2008).

Food shortages for marine birds occur every few years in conjunction with ENSO events. In addition to increased SSTs, these events precipitate lowered ocean thermoclines and weakened upwellings; these changes, in turn, lead to decreases in surface water productivity and the movement of surviving forage fish to deeper water. For gulls and other non-diving seabirds that feed on fish, the paucity of available food results in less energy intake for parents and young, and may lead to longer foraging bouts. Reproductive failure and population declines often follow (Barber and Chavez 1983, Schreiber and Schreiber 1984, McGowan et al. 1998, Stenseth et al. 2002). Rises in SST due to climate change are leading to similar changes in some regions (Grémillet and Boulinier 2009).

Although numerous studies have linked ENSO events with lowered reproductive success in marine birds (Ainley et al. 1986, Verbeek 1988, Surman and Nicholson 2009), we are unaware of previously published data that link ENSO with cannibalism in birds. Here we used logistic regression and an information-theoretic approach to test the null hypothesis that egg cannibalism and hatching success were independent of local ENSO-related SST rises at a colony of Glaucous-winged Gulls (*Larus glaucescens*) and Glaucous-winged × Western Gull (*L. glaucescens × occidentalis*) hybrids in Washington State during 2006–2011.

METHODS

Study Site and Data

Our study was carried out at Protection Island National Wildlife Refuge (48°07′40″N, 122°55′3″W), Jefferson County, Washington, USA. Protection Island is a breeding site for more than 70% of the seabirds in Washington's inland waters (Hirsch, personal observation, as cited by Galusha et al. 1987). The island lies at the southeastern corner of the Strait of Juan de Fuca and consists of a high plateau bordered by steep bluffs. Violet Point, a gravel spit extending to the southeast, supports a breeding colony of more than 2,400 pairs of Glaucous-winged Gulls and Glaucous-winged × Western Gull hybrids (Moncrieff et al. 2013). Gulls in the colony nest in narrow, linear clumps (along the beach or ditches along an old road), or in broad rectangular clumps constrained by favorable habitat. To sample all nesting habitats, we selected five rectangular sample plots (Figure 1, Plots A–E). Plot dimensions varied and were designed to include most of the nests clumped at each location. The combined sample area measured 4,205 m². The larger colony extends throughout much of the western half of the spit (Cowles et al. 2012).

We monitored the sample plots on foot daily, in the late afternoon, throughout each laying season, late May to mid-July, 2006–2011. Upon clutch initiation, each nest was marked with a 60-cm–long numbered, wooden stake. The stake was placed within 1 m of the nest and positioned so as to avoid interfering with the activities of territory occupants. Each staked nest was checked daily for new eggs, which were marked with permanent ink at their apices and in order of their laying. We monitored each nest

FIGURE 1. Sample Plots (**A–E**) located in the gull colony on Violet Point, Protection Island. The larger colony extends throughout most of western half of the spit in lightly-shaded areas east, north, and south of the marina.

until the fate of each egg was recorded as cannibalized, eagle depredated (see below), addled, died during pipping, hatched, or other (punctured, nest flooded, or rolled out of nest). For each nest, we determined the distance from its center to the center of the nest of its "nearest neighbor" (Patterson 1965) using a tape measure or laser rule (2006–2010), or a Trimble GPS and ArcGIS Desktop 10 with the "pointdistances" tool in Geospatial Modeling Environment software (2011). We also recorded the habitat type, each of which was readily distinguishable from all others: short or sparse vegetation (non-vegetated substrate or vegetated substrate without American dune grass, *Leymus mollis,* or gumweed, *Grindelia integrifolia*); by a shrub (most commonly gumweed) or a log but not on the beach; beach (cobble and/or log-strewn area from water to base of the short ∼0.5-m–high bluff bordering the beach); and beside or in tall grass (American dune grass). In 2007–2011 the mass of each egg was measured on the day it was laid using a 400-g capacity Ohaus Scout Pro SP401 portable electronic balance.

Average SST for the nine months (September–May) prior to each three-month egg-laying and chick-rearing season was calculated using data from the National Oceanographic and Atmospheric Administration's (NOAA) Port Townsend, Washington, buoy (PTWW1), located 12 km east of the study site. The September–May average was chosen a priori because 1) large-bodied seabirds such as gulls are primarily capital breeders with breeding success predicated in part on resource availability before egg production (Hodder and Graybill 1985, Boersma 1998, Marra et al. 1998, Blight 2011); and 2) a time lag occurs between changes in the physical environment and responses by seabird populations partly as a result of bottom-up control in plankton-based marine food webs (Walther et al. 2002, Grémillet and Boulinier 2009). Depending on the system, the length of the time lag may vary from days to decades (Boersma 1998) and is unknown for the system supporting Protection Island residents. Gulls leave the island in late September and October and egg production begins in late May (personal observation). In the absence of specific data concerning the length of the time lag, we considered the September–May average SST a reasonable measure of the prebreeding-season oceanic conditions that impact the local marine food web (Ramos et al. 2002).

El Niño conditions, which created warmer-than-average SSTs, preceded the 2007 and 2010 breeding seasons (Table 1). Local SSTs preceding the 2006 nesting season also were moderately warmer than average, despite the fact that NOAA's Oceanic Niño Index (ONI), based on more widespread oceanic conditions, did not classify this time period as part of an official El Niño event (National Oceanographic and Atmospheric Administration 2012).

Determination of Egg Predators
Only three Protection Island predators are known to feed on gull eggs: Bald Eagles (*Haliaeetus leucocephalus*), cannibalistic gulls, and Northwestern Crows (*Corvus caurinus*). River otters (*Lutra canadensis*), often seen running through the colony, feed on gull chicks (Hayward et al. 1975), but we never have observed them feeding on gull eggs. Bald Eagles are voracious egg predators; they hop

TABLE 1. Mean laying dates, sea surface temperatures (SSTs), and fates of gull eggs at the Protection Island breeding colony, 2006–2011. Average SSTs are from September to May prior to egg laying.

Year	Mean laying day	SST (°C)	Cannibalized	Depredated	Addled	Died pipping	Other	Hatched	n
2006	16 June	9.12	96 (20.6)	31 (6.7)	24 (5.2)	0 (0)	18 (3.9)	297 (63.7)	466
2007	12 June	9.18	200 (41.8)	24 (5.0)	24 (5.0)	3 (0.6)	16 (3.3)	211 (44.1)	478
2008	17 June	8.61	94 (16.8)	11 (2.0)	48 (8.6)	2 (0.4)	27 (4.8)	378 (67.5)	560
2009	9 June	8.68	93 (14.4)	65 (10.0)	48 (7.4)	6 (0.9)	1 (0.0)	436 (67.3)	649
2010	13 June	9.33	144 (22.5)	100 (15.6)	35 (5.5)	6 (0.9)	19 (3.0)	335 (52.4)	639
2011	9 June	8.78	100 (16.5)	11 (1.8)	40 (6.6)	9 (1.5)	17 (2.8)	429 (70.8)	606

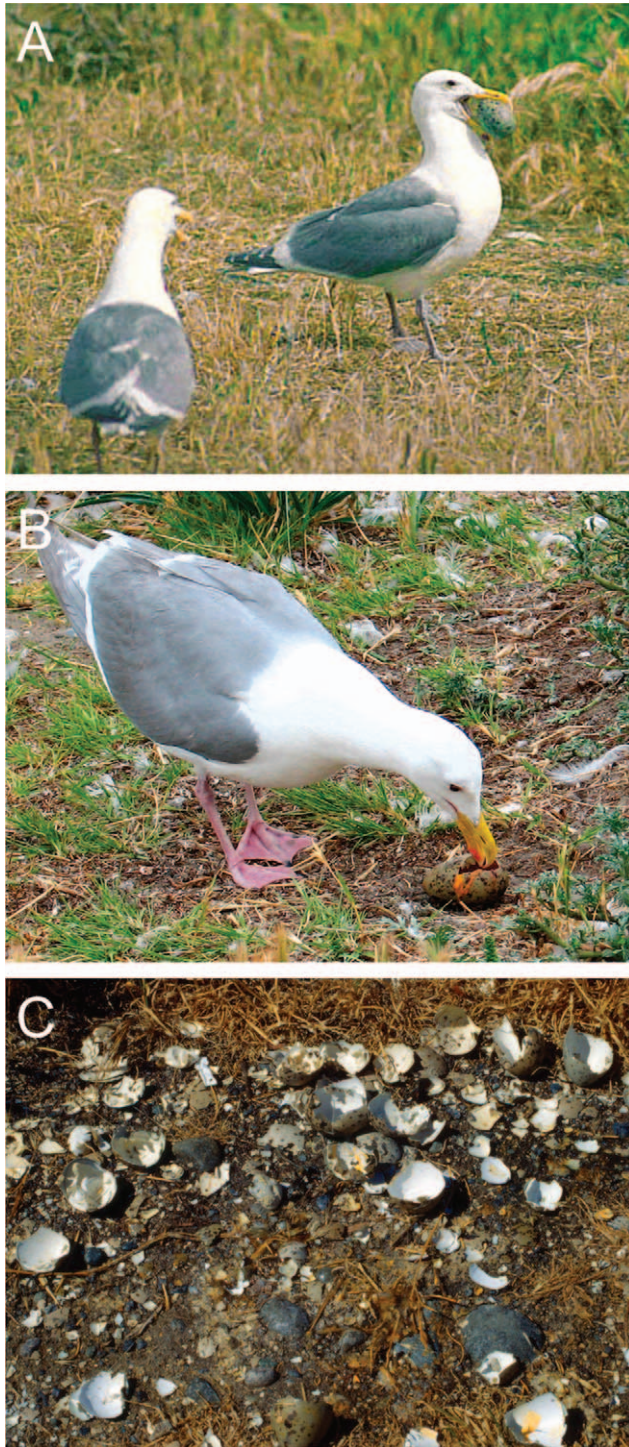Percentages of yearly totals are shown in parentheses.

FIGURE 2. (**A**) Egg cannibal has just robbed an egg from a nest and is about to fly to its own territory; facing bird vocalizes an alarm. Egg robbing events such as this happen quickly. The egg will remain unbroken until the cannibal has moved out of the robbed territory. (**B**) Egg cannibal devours the contents of an egg. (**C**) Territory of an egg cannibal feeding specialist littered with broken eggshell.

from nest to nest feeding on every egg encountered, sometimes destroying entire subareas of the colony (Thompson 1989, Hayward et al. 2010). Eagle-depredated nests are identified easily as those in which all eggs have been destroyed and which are accompanied by scattered eggshell fragments. At times, eagle-depredated nests are accompanied by adult gull remains. Gull cannibals, by contrast, commonly fly to nests of conspecifics during disturbances, quickly grab a single unprotected egg, and fly to their own nests before devouring the stolen egg; alternately, cannibals walk out of the robbed territory carrying a single egg which they eat outside the territory (Figure 2). Gull-depredated nests thus lose only one egg per predation event and typically are not associated with scattered eggshell fragments. Similarly, Northwestern Crows take single unprotected gull eggs from nests and remove them from the territory to feed (Verbeek 1988, Verbeek and Butler 1999). Because of this similarity between the behavior of gull cannibals and crows, it is impossible to distinguish between the effects of these two predators without actually observing the predation events. During thousands of hours of observation of the Violet Point colony, however, we saw numerous egg cannibalization events, but we never saw a crow take an egg from a nest. Thus, we believe that crow depredation was a relatively rare event on this colony. This interpretation is consistent with evidence provided by Burger (1980), who found that during a 2-hr observation period Herring Gull (*Larus argentatus*) cannibals devoured 44 of 45 eggs placed in artificial nests, whereas a crow took only one egg (Burger 1980). It also is consistent with a report by Good (2002), who observed extensive egg depredation by colony residents at a Glaucous-winged × Western Gull colony. Consequently, we attribute losses of single eggs to gull depredation, but recognize the possibility that crows and eagles were responsible for a small fraction of these losses.

Logistic Regression Analysis

For the 2007–2011 breeding season data ($n = 2,932$ eggs) we used logistic regression (Hosmer and Lemeshow 2000) to analyze the binary outcomes of cannibalism (0 if the egg was not cannibalized, and 1 if the egg was cannibalized) and of hatching success (0 if the egg did not hatch, and 1 if the egg hatched). Cannibalism and hatching success were considered functions of SST, egg mass (MASS), nearest-neighbor distance (NN), number of days before or after the mean laying date (Table 1) for the season (DAYS), sample area (PLOT), habitat type (HAB), egg order (ORDER), and total number of eggs laid in the nest (CSIZE); see Supplemental Material Table S1 for the coding details for each of the four categorical variables (PLOT, HAB, ORDER, and CSIZE). We regressed the log-odds of cannibalism and hatching on these eight factors as well as on 17 interaction terms between PLOT and HAB (three

of the 20 possible combinations did not occur; see Table 2) with an intercept term. We did not include the 2006 data in this phase of the analysis because of the absence of egg mass measurements.

For cannibalism and separately for hatching success, we obtained a suite of alternative models by taking all possible linear combinations of the eight factors, with intercepts. The interaction terms were included for those models with both PLOT and HAB variables. We took an information-theoretic approach to parameter estimation and model selection (Burnham and Anderson 2002). In particular, we found parameter estimates and computed the Akaike Information Criterion (AIC) for the global model and all submodels. We ranked the factors SST, MASS, NN, DAYS, ORDER, CSIZE, PLOT, and HAB in order of importance using Akaike weights (Burnham and Anderson 2002). The Akaike weights also were used to compute a weighted average for each parameter estimate over all of the models containing that parameter. Model-averaged parameter estimates are more stable than those associated with any one model because they account for the uncertainty in model selection (Burnham and Anderson 2002). We computed odds-ratios from the model-averaged parameter estimates.

Model Performance Analysis

To test the capability of model prediction, we used the AIC to select the best cannibalism and hatching success models from their respective suites of parameterized alternatives. To measure the goodness-of-fit and validate the selected models we followed the assessment recommended by Giancristofaro and Salmaso (2003) for logistic regression models. Given that the factor MASS did not appear in the selected models for either cannibalism or hatching success (see Results), we included the 2006 egg data, for which MASS was not available, to obtain a larger dataset (2006–2011, $n = 3,398$) for validation. This both increased the power of any hypothesis test and provided data points in the validation set that had not been used for the model selection. The egg data were split into two randomly chosen samples: 75% for parameter estimation ($n = 2,548$) and 25% for model validation ($n = 850$). The selected models were fitted to the larger sample and then model performance was measured on both samples. Using a larger portion for fitting helps avoid problems with quasi-complete separation of variables. This data-splitting process was repeated 100 times. The performance was measured by three indicators, one for discrimination (how well the model predicted the chance of cannibalism [or hatching] to be greater than 50% rather than less than 50% when the observed frequency was greater than 50%, and vice versa) and two for calibration (how close the predicted probability was to the observed). Discrimination was measured by the C-statistic defined by Giancristofaro

TABLE 2. Number of eggs by plot and habitat type, 2007–2011.

Plot	Short/sparse vegetation	Beside shrub/log	Beach	Beside/in tall grass	n
A	14	107	14	277	412
B	153	150	0	179	482
C	340	216	437	14	1,007
D	202	239	91	0	532
E	239	214	46	0	499
Total	948	926	588	470	2,932

and Salmaso (2003) with values between 0.8 and 0.9 indicating excellent discrimination, values between 0.7 and 0.8 indicating acceptable discrimination, and a value of 0.5 indicating no discrimination. Calibration was measured by bias (the difference in average predicted probabilities and average observed outcomes) and by Hosmer and Leme-show's (2000) goodness-of-fit statistic $\hat{C}$ with 10 groups. Bias is minimized by logistic regression (relative to the data set being fit) and thus would be approximately zero on the samples to which the model was fitted; a small increase in bias on the validation samples would indicate successful model validation, whereas a substantial increase in bias would call into question the predictive value of the model. The $\hat{C}$ statistic follows a chi-square distribution with $df = 8$ and rejection indicates a lack of fit.

RESULTS

Egg Fates 2006

Cannibalism was consistently the most important cause of egg loss. Eagle depredation and addling were less important, followed by death during pipping and other causes. Hatching success was higher than 50% during all years except 2007, which also was the year of the highest rate of cannibalism. The highest percentages of cannibalism and lowest percentages of hatching success occurred during 2007 and 2010, the two breeding seasons which followed nine months of higher-than-average ENSO-related SSTs. A moderately high level of cannibalism occurred in 2006, which followed moderately higher than average SSTs (Table 1).

AIC, Factor Importance, and Odds-Ratios

Because most egg loss was due to cannibalism, the factors involved in the best cannibalism and hatching models, as well as the factors identified in the factor importance analysis, were nearly the same (PLOT, HAB, CSIZE, DAYS, and SST), although with opposite effects (Tables 3–6). Table 3 shows the AIC results for the suite of alternative models. The cannibalism model with $\Delta AIC = 0$ for the 2007–2011 dataset was the model with all of the factors except ORDER, NN, and MASS. The hatching success model with $\Delta AIC = 0$ for the 2007–2011 dataset was the

TABLE 3. Logistic regression models of cannibalism and hatching success that have any support from the data ($\Delta QAIC_c$ <10) with Akaike weights (w_i), the number of parameters including σ^2 (κ), and the log likelihood (L). The $QAIC_c$ is the second order quasi-likelihood AIC. The global model includes the variables SST, MASS, NN, DAYS, ORDER, CSIZE, PLOT, and HAB as well as the interaction terms between PLOT and HAB.

Model	$\Delta QAIC_c$	w_i	κ	L
Cannibalism				
w/o ORDER, NN, MASS	0.00	0.22	22	−1248
w/o NN	0.12	0.20	25	−1245
w/o NN, MASS	0.26	0.19	24	−1246
w/o ORDER, NN	1.10	0.12	23	−1248
w/o ORDER, MASS	2.01	0.08	23	−1248
Global model	2.12	0.07	26	−1245
w/o MASS	2.27	0.07	25	−1246
w/o ORDER	3.10	0.05	24	−1248
Hatching Success				
w/o ORDER	0.00	0.41	24	−1736
w/o ORDER, MASS	0.87	0.26	23	−1738
Global model	2.56	0.11	26	−1736
w/o ORDER, NN	3.24	0.08	23	−1739
w/o MASS	3.97	0.05	25	−1737
w/o ORDER, NN, MASS	4.20	0.05	22	−1741
w/o NN	5.78	0.02	25	−1738
w/o NN, MASS	7.30	0.01	24	−1740

Note: w/o = without.

model with all of the factors except ORDER; however, the model omitting both ORDER and MASS was very close ($\Delta AIC = 0.87$) and had one less parameter. For both cannibalism and hatching success, we listed all other models with essentially any support (ΔAIC <10) for comparison purposes.

The overdispersion parameter estimates from the global models (1.048 for cannibalism and 1.015 for hatching success) were well within the range of values (1 to 4) that indicate a small amount of extrabinomial variation (due to demographic stochasticity and lack of independence) rather than inadequate model structure (Burnham and Anderson 2002). The model-averaged coefficients are shown in Supplemental Material Tables S2–S3, along with unconditional standard errors and model-averaged correlation coefficients. Odds-ratios and 95% confidence intervals are listed in Tables 4 and 5.

The relative factor importance for cannibalism and hatching success, based on Akaike weights, is summarized in Table 6. For cannibalism, the factors PLOT, HAB, CSIZE, DAYS, and SST were clearly important, NN was unimportant, and ORDER and MASS were fairly unimportant. For hatching success, the factors PLOT, HAB, CSIZE, SST, and DAYS were clearly important whereas ORDER was unimportant. NN was fairly important and MASS was fairly unimportant.

The odds-ratios in Tables 4 and 5 give the following results: Increases in average sea surface temperature prior

TABLE 4. Cannibalism odds-ratios (OR) with 95% confidence intervals (CI) associated with a *c* unit increase in the factor or, in the case of design variables, relative to the given reference variable. Habitats are short or sparse vegetation (SV), beside shrub or log (SL), beach (BC), and beside or in tall grass (TG).

Factor	*c*/reference	OR	95% CI
MASS	5 grams	0.96	(0.89, 1.03)
SST*	0.1 deg	1.10	(1.06, 1.13)
NN	100 cm	0.99	(0.92, 1.07)
DAYS*	1 day	1.09	(1.06, 1.11)
CSIZE	1 egg		
2 eggs*		0.13	(0.07, 0.21)
> 2 eggs*		0.09	(0.05, 0.15)
ORDER	1st egg		
2nd egg		0.81	(0.64, 1.03)
3rd egg		0.77	(0.57, 1.03)
PLOT A	HAB SV		
HAB SL		0.90	(0.14, 5.92)
HAB BC		2.05	(0.20, 20.90)
HAB TG		1.20	(0.20, 7.04)
PLOT B	HAB SV		
HAB SL*		0.28	(0.23, 0.33)
HAB TG*		0.06	(0.04, 0.09)
PLOT C	HAB SV		
HAB SL*		0.54	(0.45, 0.63)
HAB BC*		0.68	(0.62, 0.75)
HAB TG		0.79	(0.30, 2.11)
PLOT D	HAB SV		
HAB SL*		0.28	(0.26, 0.32)
HAB BC*		0.40	(0.34, 0.48)
PLOT E	HAB SV		
HAB SL*		0.39	(0.35, 0.42)
HAB BC*		0.68	(0.54, 0.87)

* Effect of variable is significant.

to egg-laying increased the odds of cannibalism and decreased the odds of hatching success. Every increase of 0.1°C increased the odds of cannibalism by 10% and reduced the odds of hatching by 10%, if all other factors were held constant.

Larger clutch sizes were associated with lower odds of cannibalism and greater hatching success. In terms of odds, an egg from a two-egg clutch was 87% less likely to be cannibalized and >6 times more likely to hatch than an egg from a one-egg clutch. An egg from a three-egg clutch was 91% less likely to be cannibalized and >7 times more likely to hatch than an egg from a one-egg clutch.

Eggs laid close to the mean laying date were less likely to be cannibalized and more likely to hatch. Each day away from this date increased the odds of cannibalism by 9% and decreased the odds of hatching success by 7%.

The farther away the nest is from its nearest neighbor, the better the odds of the eggs hatching. Every additional 1 m increased the odds of hatching by about 7%; the decrease in cannibalism was not significant.

TABLE 5. Hatching success odds-ratios (OR) with 95% confidence intervals (CI) associated with a *c* unit increase in the factor or, in the case of design variables, relative to the given reference variable. Habitats are short or sparse vegetation (SV), beside shrub or log (SL), beach (BC), and beside or in tall grass (TG).

Factor	*c*/reference	OR	95% CI
MASS	5 grams	1.05	(0.99, 1.11)
SST*	0.1 deg	0.90	(0.88, 0.93)
NN*	100 cm	1.07	(1.01, 1.13)
DAYS*	1 day	0.93	(0.90, 0.95)
CSIZE	1 egg		
2 eggs*		6.11	(3.51, 10.63)
> 2 eggs*		7.38	(4.31, 12.65)
ORDER	1st egg		
2nd egg		1.11	(0.92, 1.35)
3rd egg		1.09	(0.86, 1.38)
PLOT A	HAB SV		
HAB SL		0.27	(0.05, 1.50)
HAB BC		0.15	(0.02, 1.07)
HAB TG*		0.13	(0.02, 0.69)
PLOT B	HAB SV		
HAB SL*		2.82	(2.46, 3.24)
HAB TG*		2.17	(1.93, 2.44)
PLOT C	HAB SV		
HAB SL*		1.99	(1.80, 2.20)
HAB BC*		0.77	(0.73, 0.81)
HAB TG		0.95	(0.49, 1.86)
PLOT D	HAB SV		
HAB SL*		3.30	(3.02, 3.60)
HAB BC		0.96	(0.84, 1.11)
PLOT E	HAB SV		
HAB SL*		2.19	(2.02, 2.38)
HAB BC*		0.62	(0.48, 0.80)

* Effect of variable is significant.

TABLE 6. Relative factor importance for cannibalism and hatching success.

Factor	Importance
Cannibalism	
PLOT	1.00
HAB	1.00
CSIZE	1.00
DAYS	1.00
SST	1.00
ORDER	0.54
MASS	0.45
NN	0.27
Hatching Success	
PLOT	1.00
HAB	1.00
CSIZE	1.00
SST	1.00
DAYS	1.00
NN	0.84
MASS	0.62
ORDER	0.20

In general, eggs in non-beach nests beside a shrub or log were at the greatest advantage. An egg in this habitat exhibited the lowest odds of being cannibalized, except in Plot B, in which eggs in tall grass were even less likely to be cannibalized, and in Plot A, in which the decrease was insignificant. An egg in this habitat also had the highest odds of hatching, except in Plot A, in which there was a nonsignificant decrease.

For avoiding cannibalism, the next best habitat was the beach, which was always better than sparse vegetation, except in Plot B which had no beach, and in Plot A in which no habitat was significantly superior or inferior to another.

For hatching success, the next best habitat was sparse vegetation except in Plot B, in which tall grass was significantly better than sparse vegetation. Beach habitat was significantly inferior for hatching success in Plots C and E, and tall grass was a disadvantage for hatching success in Plot A.

Model-Performance Analysis

To test the capability of model prediction, we performed validation procedures on one cannibalism model and one

hatching success model. The best model for cannibalism was the model without ORDER, NN, and MASS (ΔAIC = 0; Table 3). For hatching success, we selected as the best model the one without ORDER and MASS (ΔAIC = 0.87 and one less parameter than the model with AIC = 0; Table 3). Given that the selected models did not include MASS and the 2006 data did not include mass measurements, we combined the 2006 data with the 2007–2011 data for the purpose of model validation.

The selected models performed reasonably well, with stability in the parameters that builds confidence in the predictions made based on these models. The details of the validation results are in the Supplemental Material.

Note that the odds-ratios and factor importance analysis (Tables 4–6) were based on model-averaging over all the alternative models on the 2007–2011 data in order to reflect the still-present level of model uncertainty, whereas the model performance analysis for validation and prediction was based on the selected, individually parameterized models.

DISCUSSION

We have demonstrated a positive relationship between egg cannibalism and local SST, and a negative relationship between hatching success and local SST at a colony of Glaucous-winged Gulls and Glaucous-winged × Western Gull hybrids. Other influential factors included location of a nest within the colony, habitat type, clutch size, and number of days to or from mean laying date.

Cannibalism directly affects the fitness of individuals and dynamics of populations (Dong and Polis 1992). Modeling studies and empirical data show that nonlinear

effects of cannibalism on population dynamics can include cycles and even chaotic fluctuations (Mertz and Davies 1968, Hastings and Costantino 1987, Orr et al. 1990, Cushing et al. 2002). Other studies suggest that cannibalism of juveniles by adults can allow populations to survive times of low resource levels by redirecting reproductive effort to times when resource levels are high (Elgar and Crespi 1992). Van den Bosch et al. (1988) and Cushing (1991) used mathematical models to show that cannibalism can serve as a "lifeboat" mechanism when adult resource is low and juveniles consume a resource inaccessible to adults. Henson (1997) extended those results to show that cannibalism can allow a population to survive times of low resource even if juveniles and adults depend on the same resource.

Cannibalism commonly is observed among colonial seabirds, especially among adult gulls that steal eggs and chicks from other colony inhabitants (Paynter 1949, Tinbergen 1961, Patterson 1965, Drent 1970, Parsons 1971, 1975, Davis and Dunn 1976, Burger 1980). Stanback and Koenig (1992) suggested that a motivating factor for egg and chick cannibalism among gulls is nutritional benefit, but they did not link this behavior directly with impoverished food supply. Fordham and Cormack (1970), however, found that adult Kelp Gulls (*L. dominicanus*) killed more chicks when colony food supply was low, and Hunt and McLoon (1975) attributed this increased infanticide to a tendency for chicks to wander into neighboring territories when they were unable to obtain food from parents. Neither Fordham and Cormack (1970) nor Hunt and McLoon (1975) mentioned egg cannibalism. To our knowledge, no previous study has linked egg cannibalism in birds with low food supply.

The highest percentages of cannibalism occurred during 2007 and 2010, nesting seasons preceded by higher than average SSTs linked with ENSO episodes; a moderately high level of cannibalism also occurred in the 2006 season, which was preceded by somewhat higher than average local SSTs not part of an official ENSO episode. Egg cannibalism in response to these sea-surface warming events provides a low-cost, readily available energy source for hungry birds. Based on an average mass of 93.6 g per egg ($n = 2,932$ eggs weighed 2007–2011), and an energy content of 6.7 kJ/g for whole gull eggs (Ricklefs 1977), each cannibalized egg on Protection Island contained approximately 627 kJ of food energy, more than half the daily energy requirement of a resident gull based on estimates for similarly-sized Herring Gulls (Norstrom et al. 1986).

We found that a 0.1°C increase in SST increased the odds of cannibalism by 10%. High quality, annually resolved records of sea surface temperature based on growth rings in geoduck clams (*Panopea abrupta*) indicate that sea surface temperatures in the Strait of Juan de Fuca increased approximately 1°C between 1950 and 1998

(Strom et al. 2004). Predictions suggest this warming trend will continue; moreover, this region has warmed at a higher rate than the global warming trend (Snover et al. 2005). Although a 1°C change in SST is beyond the scope of the temperature variability in our dataset, extrapolation based on the parameterized model produces an odds ratio of 2.50 for this change, suggesting that a 1°C increase in SST would increase the odds by 150% that an egg will be cannibalized. Prior to our study, few data have been available on the frequency of egg cannibalism among gulls in this region. One exception is a dataset from nearby Mandarte Island, British Columbia, where only 5.0% (83 of 1,652) of sample Glaucous-winged Gull eggs were lost or eaten in 1961 and 1962 (Vermeer 1963). A second study on Mandarte Island in 1979 and 1980 found that 5.6% (26 of 466) of sample eggs were lost or eaten (Verbeek 1986). By contrast, from 2006 to 2011, we found that 28.5% (967 of 3,397) of sample eggs on Protection Island were lost or eaten, including the 240 eggs presumably lost to eagle predation (Table 1). To what extent, if any, increasing SSTs contributed to the much higher egg loss on Protection Island is unknown.

Eggs appearing early or late relative to the mean date of laying were more likely to be cannibalized and were less likely to hatch. This is consistent with the Fraser Darling effect, the hypothesis that seasonal synchronization of egg laying leads to predator satiation, reducing the chance that any individual egg will be lost (Darling 1938). Furthermore, eggs appearing late relative to the mean date of hatching tend to be laid by younger parents which, up to the age of 12 years old, experience lower hatching success on this colony (Reid 1988).

We found that larger clutch sizes were associated with lower odds of cannibalism and greater hatching success. Murphy et al. (1992) also showed a strong association between clutch size and hatching success in this species. This could be due to better parental care; for example, Reid (1988) found that older, more experienced breeders on average produced slightly larger clutch sizes, although this association did not appear to be strong. Alternately, benefits associated with larger clutch sizes could be due to differential cannibalism rates on eggs in nests with different numbers of eggs; for example, if cannibals randomly choose a nest (regardless of the number of eggs in it) and randomly choose one egg within the nest, then an egg in a nest with more eggs has less chance of being cannibalized. With regard to this second possibility, however, it is important to note two facts. First, the clutch size factor was the number of eggs laid, not the number of eggs in the nest when an egg was cannibalized. Second, in this study the egg, rather than the nest, was the experimental unit; that is, we assumed that if all factors were held constant, each egg was equally likely to be cannibalized. Indeed, we suspect that the benefit of larger

clutch size is due to better parenting, because cannibalism tended to occur during disturbances and appeared to be largely opportunistic on unattended nests. In any event, all confounding effects leading to non-independence of eggs in the same nest were addressed by the overdispersion analysis, and the overdispersion parameter estimates indicated a relatively small effect from lack of independence (see Results).

Cannibalism and hatching success were affected strongly by nest habitat type. Dominant landscape features such as logs and shrubs offer shading and wind protection to eggs, thus facilitating hatching success (Pierotti 1982, Pierotti and Good 1994); eggs laid near these features are less visually exposed than those laid in more open habitat (Burger 1972, Good 2002). Moreover, logs and shrubs inhibit maneuverability by fast-moving cannibals attempting to avoid attack by territory owners. Our Plot B contained more tall grass habitat than any of the five experimental plots; eggs in nests located beside or tunneled within tall grass within this plot were much less likely to be cannibalized than eggs in other, more visually accessible habitats (see also Burger and Shisler 1978, Burger and Gochfeld 1981, 1985, Hayward 1993, Hayward et al. 2000, Good 2002). Eggs in this habitat, however, seemed especially attractive to Bald Eagles where the tall grass prevented diving gulls from striking the eagles' heads from above (Hayward et al. 2010).

Plot location played a significant role in our study even when controlled for habitat type. This may be due to complex interactions among per-plot habitat proportions, numbers of eagle disturbances, and differences in access to beach and water (personal observation). With respect to the latter possibility, Hand et al. (1981) found that Western Gulls nesting close to water were able to make quick trips to bathe and drink without leaving eggs and chicks unattended for long periods.

Cannibalism accounted for the highest proportion of egg deaths during all six years of this study (Table 1), including years when food was abundant. Thus, poor food supplies only increased the incidence of an otherwise standard behavior. Individual gulls nesting on Violet Point tend to function as feeding specialists, with some individuals specializing on blue mussels, others on cockles, and others on crustaceans (personal observation). Analysis of regurgitated boli (Lindborg et al. 2012) and detritus associated with territories at this colony suggest that landfill waste plays only a minor role in the diets of these birds. During the incubation period, a small ($<1\%$) but persistent proportion of resident gulls specialize on stealing and eating eggs from fellow residents. Territories of egg cannibal specialists are easily identified as those littered with large deposits of fragmented eggshell (Hayward et al. 2000). We do not know if, during our study, egg cannibal specialists increased the frequency of cannibalism when food supplies were low, or if higher proportions of the residents engaged in cannibalism during these times. No increase in the quantity of eggshell on cannibal territories was noted when egg loss due to cannibalism was high, so we suspect that higher proportions of gulls acted as cannibals. This is consistent with a well-substantiated prediction of foraging theory that consumers broaden their diets beyond their usual limits when food is scarce (Dong and Polis 1992). Given that most gulls will cannibalize eggs opportunistically when available (Burger 1980, Good 2002), increases in cannibalism may in part result from increased opportunity created by a reduction in territory attendance by neighboring gulls engaged in longer foraging trips.

Marine-nesting gulls are important indicator species (Blight 2011, Kershner et al. 2011). We do not know if increased levels of cannibalism in response to higher SSTs, documented here for gulls, occur in other seabirds. Moreover, it is unclear how such an increase might impact overall population trends. Gulls are multiyear breeders; if they experience reproductive failure during one or several ENSO-related events, they typically have other opportunities to breed. In the case of rising SSTs associated with climate change, however, increasing levels of cannibalism could lead to declining populations in the absence of compensatory adaptive modifications or range shifts.

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