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Every-other-day clutch-initiation synchrony as an adaptive response to egg cannibalism in Glaucous-winged Gulls (*Larus glaucescens*)

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ABSTRACT—Sea surface temperatures (SST) in the Pacific Northwest of North America rose 1 °C during the last half of the twentieth century. Cannibalism, a behavior observed in diverse taxa, is often associated with low food supplies, which for marine animals can be precipitated by high SSTs. In an 8 year study, we found that in years of higher sea surface temperatures, Glaucous-winged Gulls (*Larus glaucescens*) breeding in a colony in Washington State, Salish Sea, USA, tended to exhibit higher rates of egg cannibalism by males, higher levels of every-other-day clutch-initiation synchrony by females, and longer egg-laying seasons than in years of lower SST. Clutch-initiation synchrony increased the odds that an egg survived cannibalism and may serve as an adaptive response to egg cannibalism. Short-term climate and resource fluctuations associated with El Niño Southern Oscillation (ENSO) events may select for behavioral plasticity in marine organisms, allowing long-lived individuals such as marine birds to switch between alternative life history tactics. The implications for long-term SST warming, however, remain unknown. *Received 26 July 2019. Accepted 8 December 2020.*

Key words: climate change, conspecific predation, egg-laying synchrony, El Niño Southern Oscillation (ENSO), seabird colony, sea surface temperature (SST).

Sincronía en la iniciación de la puesta en días alternos como respuesta adaptativa al canibalismo de huevos en la gaviota *Larus glaucescens*

RESUMEN (Spanish)—Las temperaturas de superficie marina (SST) en el Pacífico noroeste de Norteamérica aumentaron 1 °C durante la segunda mitad del siglo XX. El canibalismo, un comportamiento observado en diversos taxa, frecuentemente se asocia con baja disponibilidad de alimentos, la cual puede exacerbarse en animales marinos por una SST elevada. En un estudio de 8 años, encontramos que en los años con las más altas SST, las gaviotas *Larus glaucescens* que anidan en una colonia en el Mar de Salish en el estado de Washington, EUA, tendieron a sufrir mayores tasas de canibalismo de huevos por machos, tuvieron niveles más altos de sincronía en el inicio de la puesta en días alternos por parte de las hembras y temporadas más largas de puesta que aquellas de años con más bajas SST. La sincronía en el inicio de la puesta aumentó la probabilidad de que un huevo sobreviviera el canibalismo y podría ser una respuesta adaptativa al canibalismo de huevos. El clima a corto plazo y las fluctuaciones en recursos asociados a eventos de El Niño podrían seleccionar la plasticidad conductual en organismos marinos, permitiendo individuos longevos como las aves marinas alternar entre tácticas en sus historias de vida. Las implicaciones de las SST a largo plazo, sin embargo, siguen siendo desconocidas.

Palabras clave: cambio climático, colonia de aves marinas, depredación conespecífica, El Niño, sincronía en la puesta de huevos, temperatura de la superficie marina.

Cannibalism in marine food webs often is associated with food shortages, such as those caused by El Niño Southern Oscillation (ENSO) events (Dong and Polis 1992, Alheit and Niquen 2004, Guevara-Carrasco and Lleonart 2008). ENSO events trigger increased sea surface temperatures (SST), weakened upwellings, lower thermoclines, and concomitant decreased plankton productivity. Forage fish follow plankton to deeper water and decrease the food supply for non-diving seabirds, leading to reproductive failures and population declines (Murphy 1936, Barber and Chavez 1983, Schreiber and Schreiber 1984, Ainley 1994, Ainley et al. 1994, 1995; McGowan et al. 1998, Stenseth et al. 2002, Smith et al. 2017).

At Protection Island National Wildlife Refuge located in the Salish Sea, Washington, USA, Hayward et al. (2014) examined the effect of local SST on cannibalism in a colony of ~2,000 pairs of Glaucous-winged Gulls (*Larus glaucescens*). They found that cannibalism by adult gulls on other colonists' eggs increased and hatching success decreased with rises in SST. In particular, a 0.1 °C rise in SST was associated with a 10% increase in the odds that an egg would be cannibalized. They also noted that 1 egg contains almost half the energy required per day by an adult gull and suggested that egg cannibalism might be adaptive

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during years of high SST and its associated low resource availability.

In a second study on the same Glaucous-winged Gull colony, Henson et al. (2010) demonstrated the existence of every-other-day egg-laying synchrony in sufficiently dense areas of the colony during some years. Glaucous-winged Gulls lay eggs approximately every other day until completing 2- or 3-egg clutches. Egg-laying synchrony is manifested as an every-other-day spike in the number of eggs laid per day on the colony. Henson et al. (2010) also showed that egg-laying synchrony was strongest for clutch initiations; that is, female gulls tended to lay their A-eggs synchronously (on the same day) with other females. (First, second, and third eggs laid in a clutch are designated as A-, B-, and C-eggs, respectively.) Mathematical models suggested that synchronization would be associated with longer clutch-initiation seasons than seasons without synchronization (Henson et al. 2011).

Henson et al. (2011) posed, but did not test, the hypothesis that egg-laying synchrony is an adaptive response to egg cannibalism, and suggested that if more eggs are laid on the same day, each egg has a lower chance of being cannibalized. In particular, clutch-initiation synchrony could be adaptive if (1) A-eggs are cannibalized more heavily than B- or C-eggs, and (2) A-eggs tend to be cannibalized on the same day they are laid. In this case, clutch-initiation synchrony would be adaptive if the odds of a given A-egg being cannibalized on the day it is laid is a decreasing function of the number of A-eggs laid on that day. If this hypothesis is true, one would expect clutch-initiation synchrony to be strongest during years of high levels of egg cannibalism, that is, during years of high SST.

On the basis of this hypothesis we tested the following predictions: (1) the A-egg in a clutch is more likely to be cannibalized than the B- or C-egg, (2) the A-egg in a clutch is most likely to be cannibalized within the first 24 h after it was laid, (3) the odds that the A-egg is cannibalized within the first 24 h is a decreasing function of the number of A-eggs laid that day, and (4) the degree of clutch-initiation synchrony increases with SST, concomitantly with high degrees of egg cannibalism. We also tested the prediction that the length of the clutch-initiation season increases with egg-laying synchrony, and thus with SST and cannibalism. Our primary objective is to demonstrate the selective advantage of egg-laying synchrony.

Methods

Location and sample plots

On Violet Point at Protection Island National Wildlife Refuge, Washington, USA (48°07′40″N, 122°55′3″W), we monitored all Glaucous-winged Gull nests in sample plots centered on dense, socially cohesive groups. During 2006–2008 we used 5 sample plots, Plots A–E (Fig. 1). Throughout this time, the northwest boundary of the colony moved farther west; thus in 2009–2011 we added a sixth study area to the northwest of Plot C, which we called Plot C-auxiliary (C_{aux}; Fig. 1). We did not collect relevant data in 2012–2013. During this time Plots A and B became mostly depopulated, primarily as the result of encroaching vegetation and possibly Bald Eagle (*Haliaeetus leucocephalus*) predation (Cowles et al. 2012); thus in 2014 we added a new study area, Plot L, to the southeast of Plot D (Fig. 1). In 2014–2015 we continued the study in Plots C, C_{aux}, D, E, and L.

Nest monitoring

Nest monitoring methods are detailed in Hayward et al. (2014); we repeat the main points here for the convenience of the reader. We monitored the sample plots on foot daily, in the late afternoon, throughout each laying season, late May to mid-July, 2006–2011 and 2014–2015. Upon clutch initiation, each nest was marked with a wooden stake placed to avoid interference with the 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 until the fate of each egg was recorded as cannibalized, depredated by Bald Eagles (see below), addled, died during pipping, hatched, or other (punctured, nest flooded, or rolled out of nest).

Identification of causes of egg loss

During 30 years of observations of the Protection Island colony, we observed only 2 species of gull egg predators, Bald Eagles and Glaucous-winged Gull conspecifics. Bald Eagles tend to feed

Figure 1. Sample plots on Violet Point, Protection Island National Wildlife Refuge, Washington, USA. The full colony extends throughout much of the spit.

on all of the eggs in a clutch at the nest site, leaving behind fragments of eggshell. By contrast, Glaucous-winged Gull cannibals steal only one egg from a nest, which they typically carry away whole and leave no eggshell at the depredated territory. Thus, for each egg lost during the laying season, we decided the cause of egg loss based on the number of eggs taken and the presence or absence of eggshell fragments at the nest site (Hayward et al. 2014).

Measuring local SST

Gulls are capital breeders whose reproductive success partially depends on food availability before egg-laying (Hodder and Graybill 1985, Boersma 1998, Marra et al. 1998, Blight 2011). A time lag occurs between oceanic conditions and the impact of these conditions on oceanic food webs. Thus, gulls and other seabirds are affected by oceanic conditions in advance of egg laying

(Walther et al. 2002, Grémillet and Boulinier 2009). We computed an average local SST after Hayward et al. (2014) for the 9 months (Sep–May) prior to each egg-laying season using data from the National Oceanographic and Atmospheric Administration's (NOAA) Port Townsend, Washington, buoy (PTWW1), located 12 km east of the study site.

Test of Prediction (1): Cannibalization of A-eggs relative to that of B- and C-eggs

We tallied the number of A-, B-, and C-eggs cannibalized for the 8 years of data. We used a 2×3 chi-square test to compare numbers of A-, B-, and C-eggs cannibalized, and a 2×2 chi-square test to compare the number of A-eggs cannibalized with combined numbers of B- and C-eggs cannibalized.

Test of Prediction (2): Timing of cannibalization on A-eggs

We binned the A-eggs lost to cannibalism by the number of days they survived. We used a chi-square test to compare the number of A-eggs lost in the first 24 h to expected values calculated under the assumption that A-egg loss occurred uniformly over time.

Test of Prediction (3): Adaptive value of clutch-initiation synchrony in relation to cannibalism

For each day on which a first egg was cannibalized over the 8 years of study, we recorded the total number of A-eggs laid that same day and the number of those A-eggs lost to cannibalism that same day. We used logistic regression (with Statistics Toolbox in MATLAB; MathWorks, Natick, Massachusetts, USA) to regress the log-odds that an A-egg was cannibalized against the total number of A-eggs laid (clutches initiated) that day.

Test of Prediction (4): Degree of clutch-initiation synchrony in relation to SST

We measured the degree of clutch-initiation synchrony after Henson et al. (2010); we repeat the main points of the method here for the convenience of the reader. If E_i is the number of clutches initiated in a sample plot of the colony on day i, with $E_0 = E_{D+1} = 0$ bracketing the beginning and end of clutch initiation, then the degree of daily synchrony was defined to be

$$X = \frac{\sum_{i=0}^{D} |E_{i+1} - E_i|}{2\sum_{i=1}^{D} E_i}.$$

The numerator measures the total variation of the time series; the denominator gives the total variation for any perfectly synchronous time series with the same total number of eggs. The value $X = 1$ indicates perfect synchrony, whereas $X < 1$ indicates a departure from perfect synchrony. A high X score can occur by chance. To test whether an observed X for a given plot and year is significantly greater than expected by chance, the observed X was compared to the distribution of X values generated by 10^6 Monte Carlo simulations of random clutch initiations consisting of the observed number of clutch initiations chosen from a truncated normal distribution spanning D days with the observed sample mean and standard deviation from that plot. The associated P value was the fraction of the null distribution lying to the right of the observed X value (Henson et al. 2010).

In the present study we compared the degree of synchrony X, which depends on the number of clutches, across sample plots with differing numbers of clutches. Thus, we standardized each observed X value to an equivalent standard Z value associated with a hypothetical standard 68-clutch plot. We used 68 clutches for historical reasons because that was the number of clutches in Plot C in 2006 when synchrony was first observed. Specifically, for each observed X value associated with clutch initiations spanning D days, we constructed a standard null distribution from Monte Carlo simulations of 68 random clutch initiations occurring according to a truncated normal distribution over D days with the same sample mean and standard deviation observed in the plot for which X was computed. We then transformed the observed X value to the standard Z that preserved its P value.

Test of prediction concerning the length of the clutch-initiation season in relation to SST

For each year, we combined the clutch-initiation data from all sample plots to construct an overall temporal distribution of clutch initiations. From this distribution we quantified the length of the clutch-initiation season in 2 ways. First, we

Table 1. For each of the 8 breeding seasons, first clutch initiation dates, mean clutch initiation dates, and sea surface temperatures (SST) during the 9 months (Sep–May) prior to the egg-laying and chick-rearing seasons for nests in the study plots are shown. Also, number of territories with clutches, number of eggs, number of eggs cannibalized, and percent of total eggs cannibalized 1–30 June are shown for the study plots. Data for 2006–2011 are from Hayward et al. (2014), with minor corrections.

Year of breeding season	First clutch-initiation date	Mean clutch-initiation date	Mean Sep–May SST prior to breeding season (°C)	Number of territories in study plots	Number of eggs in study plot nests	Number of eggs cannibalized in study plots	Percent of total eggs cannibalized in study plots
2006	25 May	13 Jun	9.12	199	465	93	20.0
2007	24 May	10 Jun	9.18	201	478	200	41.8
2008	1 Jun	16 Jun	8.61	226	560	94	16.8
2009	25 May	7 Jun	8.68	248	650	92	14.2
2010	25 May	10 Jun	9.33	267	639	142	22.2
2011	24 May[a]	7 Jun	8.78	231	606	98	16.2
2014	20 May	8 Jun	9.01	279	566	121	21.4
2015	20 May	5 Jun	10.15	289	721	121	16.8
TOTALS	—	—	—	1,940	4,685	961	—

[a] Extrapolated. First day on which a nest check was done was 27 May, when one 2-egg nest was present, and a C-egg was laid on 28 May. Assuming the usual 2 d interval between ovipositions, the first egg was probably laid on 24 May.

computed the number of days spanned by the first and last clutch initiations and correlated this with SST. Second, we computed the sample standard deviation of the temporal distribution of clutch initiations and correlated this with SST.

Results

Descriptive data from each year of study, including mean pre-breeding season SSTs and nest and egg numbers from sample plots, are provided in Table 1.

Prediction (1): Cannibalization of A-eggs in clutches relative to that of B- and C-eggs

The A-egg in a clutch was much more likely to be cannibalized than the B- or C-egg, as determined by 2 methods: comparison of A-, B-, and C-eggs (Table 2; $\chi^2 = 44.41$, df = 2, $P < 0.001$), and comparison of A-eggs with B- and C-eggs combined (Table 3; $\chi^2 = 41.61$, df = 1, $P < 0.001$; expected values determined in relation to the proportion of eggs in each category).

Prediction (2): Timing of cannibalization on A-eggs

In comparison with A-eggs cannibalized at a later time ($n = 347$), A-eggs were much more likely to be cannibalized within the first 24 h ($n = 136$) ($\chi^2 = 1075.8$, df = 1, $P < 0.001$; expected values determined by assuming an equal number of cannibalizations each day for the maximum of 34 days of survival for A-eggs eventually cannibalized).

Prediction (3): Adaptive value of clutch-initiation synchrony in relation to cannibalism

The odds that the A-egg was cannibalized within the first 24 h decreased 19% for each additional 5 clutches initiated that day ($P < 0.001$, OR = 0.81). Thus, clutch-initiation synchrony conferred an advantage in the presence of cannibalism.

Table 2. Comparison of numbers of cannibalized A-, B-, and C-eggs in relation to non-cannibalized counterparts during the 8 year study.

	A-eggs	B-eggs	C-eggs	Total
Cannibalized	483	299	179	961
Not cannibalized	1,394	1,340	990	3,724
TOTAL	1,877	1,639	1,169	4,685

Table 3. Comparison of number of A-eggs and non-A eggs cannibalized in relation to number of non-cannibalized eggs during the 8 year study.

	A-eggs	Non-A-eggs	Total
Cannibalized eggs	483	478	961
Non-cannibalized eggs	1,394	2,330	3,724
TOTAL	1,877	2,808	4,685

Table 4. Years for which significant clutch-initiation synchrony occurred in at least one sample plot. Average SST was determined for the 9 months (Sep–May) prior to each 3 month egg-laying and chick-rearing season. Over the 8 year study, local SST ranged from 8.61 to 10.15 °C.

Average SST	Daily synchrony	No daily synchrony
SST $\geq$ 9.01 °C	2006, 2007, 2014, 2015	2010
SST $\leq$ 8.78 °C	None	2008, 2009, 2011

Prediction (4): Degree of clutch-initiation synchrony in relation to SST

Higher levels of clutch-initiation synchrony coincided with years of high SST (Table 4; $\chi^2 = 4.18$, df = 1, $P = 0.041$). In addition, clutch-initiation synchrony trended positively with SST ($r = 0.600$; Fig. 2A).

Prediction concerning the length of the clutch-initiation season

The length of the clutch-initiation season—the number of days between the first and last clutch initiation—trended positively with SST ($r = 0.588$; Fig. 2B), and the standard deviation of the temporal distribution of clutch initiations also trended positively with SST ($r = 0.575$; Fig. 2C). The day of the year of the first clutch initiation trended negatively with increased SST ($r = –0.605$; Fig. 2D).

Discussion

We demonstrated that the A-egg in a clutch was more likely to be cannibalized than the B- or C-egg, the A-egg was most likely to be cannibalized within the first 24 h after it was laid, and the odds that the A-egg was cannibalized within the first 24 h decreased with increasing numbers of clutches initiated that day. We also showed that in years of higher SST, larger degrees of clutch-initiation synchrony and earlier and longer egg-laying seasons tended to occur than in years of lower SST, and that clutch-initiation synchrony reduced the chance that a given egg was cannibalized.

The linkages between SST and the behaviors studied in this paper are likely indirect and mediated through the food web. When ocean water is cold and well-mixed, nutrient levels remain high and plankton thrive. By contrast, when ocean water is warm and highly stratified, nutrients are depleted and plankton numbers decrease (Richardson 2008). Lower plankton abundance leads to fewer Pacific herring (*Clupea pallasii*), historically a primary forage species for Glaucous-winged Gulls (Trapp 1979, Verbeek 1979, Bishop and Green 2001). In a meta-analysis of Pacific herring populations in the California Current Ecosystem, Thompson et al. (2017) demonstrated that herring spawning stock biomass decreased from 1980 to 2013. All 6 major spawning regions in Washington State exhibited significant declines; the Olympic/Discovery Bay region, which includes Protection Island, showed a 15% decline per year, more than twice that of the other regions. Moreover, populations of Pacific sardine (*Sardinops sagax*) and northern anchovy (*Engraulis mordax*), 2 other forage fish species in the California Current Ecosystem, have virtually collapsed (Hill et al. 2016, MacCall et al. 2016).

Environmental unpredictability, such as the occurrence/non-occurrence of ENSO episodes, is known to lead to behavioral plasticity, the genetically based capacity of individuals to respond to different environments in different ways and in which early learning and memory may play a role (Bhat et al. 2015). For example, *Daphnia magna* usually avoid light, but some genotypes exhibit a genetically enhanced ability to move toward or away from light in the presence of chemicals secreted by predatory fish (De Meester 1996); western fence lizards (*Sceloporus occidentalis*) exhibit the ability to alter their microhabitat selection when moved from their natal environments to one that is foreign (Asbury and Adolph 2007); and female and male Western Gulls (*L. occidentalis*) nesting on Southeast Farallon Island during a strong ENSO episode in 1973 spent almost equal amounts of time in incubation. By contrast, in 1974 when conditions improved with lower water temperatures, females spent significantly more time incubating than males. In 1974 when males spent more time on territory than in 1973, the ratio of male to female aggressive acts was higher than in 1973 (Pierotti 1981). Our results suggest that ENSO-related climate variability and concomitant resource fluctuations select for behavioral plasticity in Glaucous-winged Gulls, allowing individuals to switch between alternative life history tactics depending on annual environmental cues such as local SST (Fig. 3). Annett and

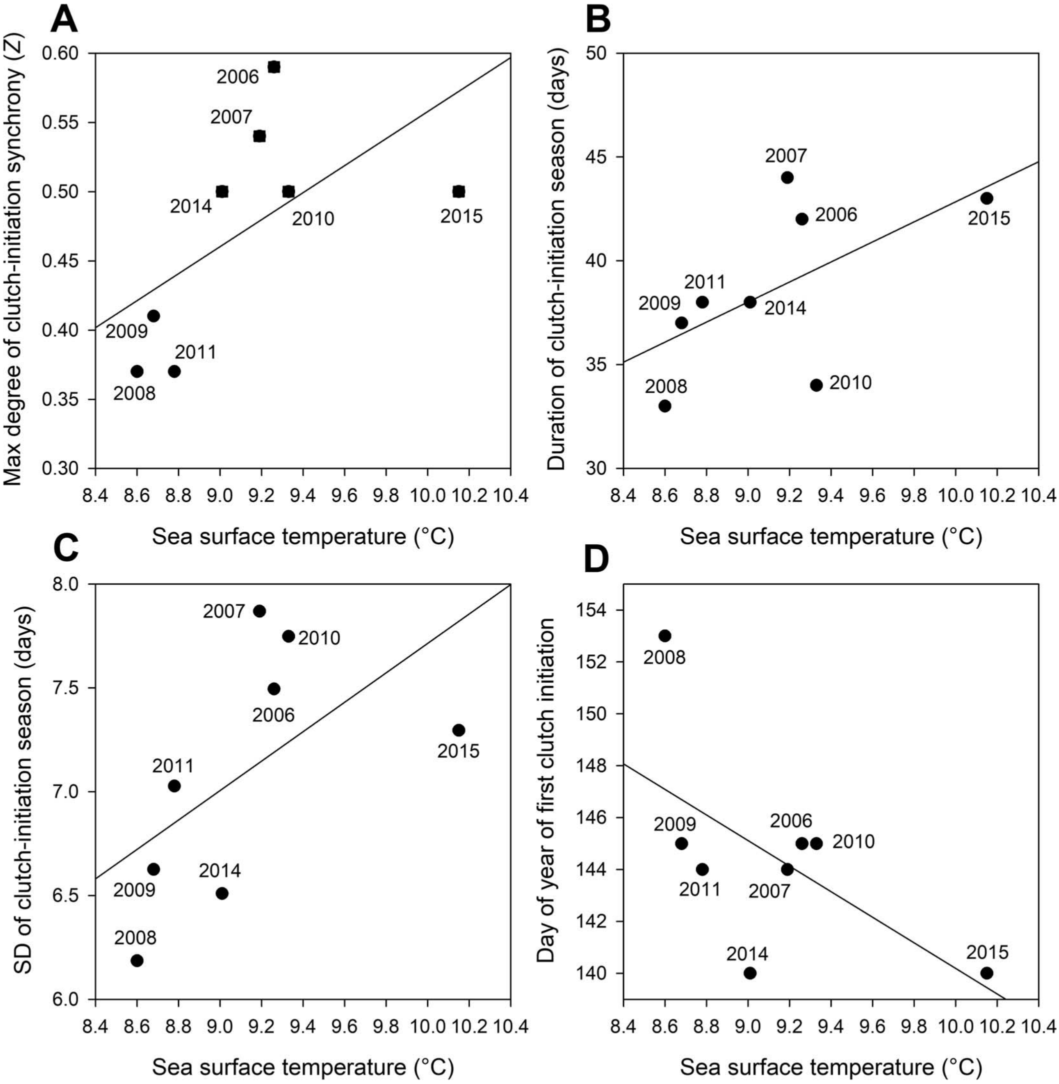

Figure 2. Characteristics of clutch initiation of Glaucous-winged Gulls in Protection Island National Wildlife Refuge, Washington, as functions of SST. (A) For each year, the maximum degree of clutch-initiation synchrony observed across all sample plots, plotted against SST. Squares indicate years in which that degree of clutch-initiation synchrony was significant. There is an increasing trend. (B) Number of days between first and last clutch initiations trends positively with SST. (C) Standard deviation of temporal distribution of clutch initiations trends positively correlated with SST. (D) Day of year on which first clutch initiation occurred trends negatively with SST.

Pierotti (1999) came to the same conclusion for Western Gulls, suggesting that foraging plasticity allows gulls to survive and even reproduce during years when more specialized feeders, such as alcids and terns, fail to do so.

The diets of Glaucous-winged Gull cannibals on Protection Island have been evaluated on the basis of regurgitated boli. In an analysis of 589 boli from this colony, Lindborg et al. (2012) found that 43.0% contained the remains of fish, 37.9% of mollusks, 27.7% of arthropods, 19.0% of eggs, 12.1% of bones, and most boli contained vegetation and inorganic material. Similar proportions were found in a combined sample of 108 boli from cannibal territories (those containing 3 or more cannibalized eggshells during the month of June)

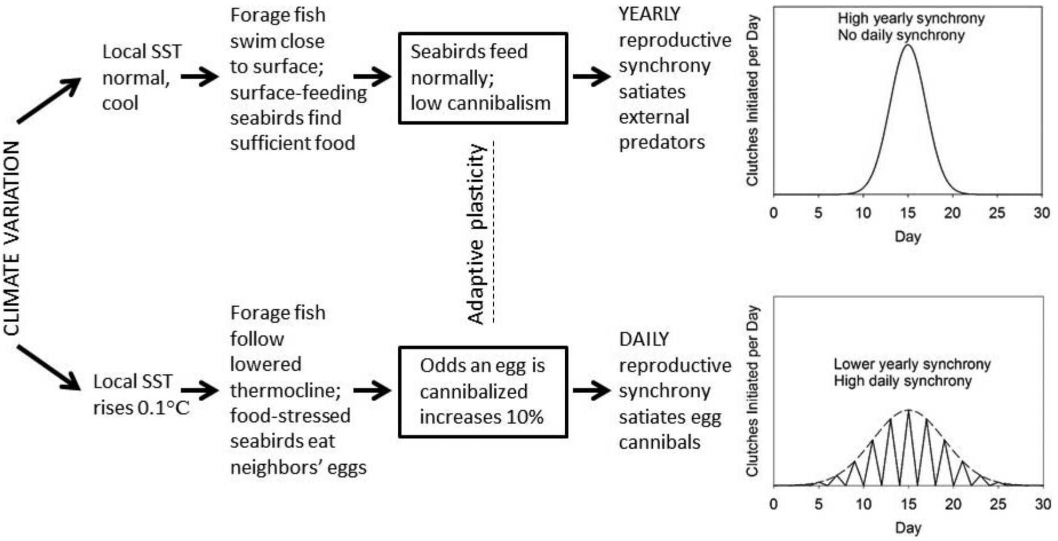

Figure 3. Conceptual model featuring alternative feeding and reproductive tactics of Glaucous-winged Gulls in Protection Island National Wildlife Refuge, Washington, predicated on local SST. Colony residents tended to switch between 2 sets of feeding and reproductive tactics depending on annual SST. In years of high SST, they exhibited high egg cannibalism, every-other-day clutch-initiation synchrony, and longer egg-laying seasons. In years of low SST, they exhibited lower egg cannibalism, no significant clutch-initiation synchrony, and shorter egg-laying seasons.

and 63 boli from non-cannibal territories; the odds of finding egg material or chick parts in cannibal boli were significantly higher than in non-cannibal boli, whereas the odds of fish parts in cannibal boli were less than in non-cannibal boli (JLH, unpubl. data). Thus, it appears that cannibals, some of which stole more than one egg per day, substituted eggs for fish as a protein source. It should be kept in mind, however, that data determinations from boli are biased toward food items containing hard parts such as bones or shells (Brown and Ewins 1996).

Reproductive synchrony on a yearly timescale, in which egg laying occurs in an annual pulse within a time window set by photoperiod (Nicholls et al. 1988), is thought to be advantageous because of external predator satiation due to a time minimization strategy (Darling 1938, James et al. 2004). Similarly, our study suggests that the every-other-day clutch-initiation synchrony may confer an advantage in the presence of egg cannibalism as hypothesized by Henson et al. (2011). Mathematical models suggested that the clutch initiation synchrony would be associated with longer egg-laying seasons (Henson et al. 2011), which is consistent with the empirically derived trend in Figure 2B. Our results suggest the hypothesis that a tradeoff occurs between protection from external predation (high yearly synchrony and short egg-laying season as postulated by Darling [1938]) and protection from conspecific predation (every-other-day clutch-initiation synchrony but longer egg-laying season, this study) (Fig. 3). It appears the tradeoff in Glaucous-winged Gulls is mediated by switching feeding tactics. The trends in Fig. 2, however, suggest that the colony as a whole did not display a distinct, dichotomous switch in tactics, but that it responded in a more continuous way (with noise) as individuals changed tactics.

Some behavioral tactics adopted during times of scarce resources delay or alter essential functions until "better times," benefits that result from behavioral plasticity. For example, Glaucous-winged Gulls on Mandarte Island, British Columbia, postponed the onset of egg-laying in response to cool weather (Verbeek 1979); Herring Gulls (*L. argentatus*) experiencing increased population density in Terschelling, The Netherlands, engaged in high rates of intraspecific chick predation (Spaans et al. 1987); and Glaucous-winged Gulls on Squab Island, Alaska, exhibited high levels of chick cannibalism when forced to feed on blue mussels (*Mytilus edulis*; Murphy et al. 1984). Indeed, individuals of many taxa respond to scarce food resources by cannibalism, which may function as a "lifeboat" mechanism by redirecting reproductive efforts to times with higher resources (Fox 1975, Polis 1981, Elgar and Crespi 1992, Henson 1997). The generalized feeding habits of gulls serve as a preadaptation for this behavior (Annett and Pierotti 1999).

Neither of the 2 sets of tactics in Fig. 3 is likely to be adaptive every year. In years of low resource availability, cannibalism may confer an advantage by enhancing adult survivorship until years of higher resource availability; but during years of high resource availability, cannibalism is unlikely to be adaptive. Indeed, our preliminary studies have shown that cannibals have lower reproductive success (JLH, unpubl. data). In years of low resource availability, clutch-initiation synchrony confers an advantage by increasing the odds that an egg survives cannibalism, but the longer egg-laying seasons associated with those years may provide less protection against interspecific predators such as eagles.

The possibility that an adaptive tactic such as egg cannibalism could contribute to the extirpation of the colony raises the question of whether individual fitness and population fitness could be in conflict, a possibility suggested by group selection experiments with flour beetles (*Tribolium castaneum*; Wade 1977, 1979). Another experiment with *Tribolium* demonstrated a case of evolutionary suicide due to an increase in the frequency of a mutant allele that increased rates of both reproduction and cannibalism, but which led to population extinction (R.A. Desharnais, unpubl. data). In the case of Protection Island gulls, an increase in the fitness of cannibalistic individuals could play a role in colony extirpation, although extirpation would most likely occur by some individuals shifting reproductive activities to other colonies. A possible decline and eventual extirpation of the Protection Island gull colony in response to egg cannibalism, however, would be compounded by the direct effect of eagle predation on gull eggs, chicks, and adults (Hayward et al. 2010, Hipfner et al. 2012, Henson et al. 2019), and by a reduction in the availability of nest habitat (Cowles et al. 2012).

Can our results shed any light on the possible effects of long-term climate warming on behavior? Average SST in the Strait of Juan de Fuca increased approximately 1 °C between 1950 and 2000 (Strom et al. 2004) and continued to rise at a rate higher than the global warming trend (Snover et al. 2005), at least until 2007 (Irvine and Crawford 2013). In Hayward et al. (2014), a 0.1 °C rise in SST was associated with a 10% increase in the odds that an egg would be cannibalized ($\beta = 0.9148$; OR = *exp*[0.9148x0.1] = 1.10; 1.10 − 1 = 0.10 = 10%). By extrapolation, a 1 °C rise would be associated with a 150% increase in the odds of cannibalism (OR = *exp*[0.9148x1] = 2.50; 2.50 − 1 = 1.50 = 150%). Although this extrapolation extends beyond the scope of the Protection Island data set, it is interesting that at a Glaucous-winged Gull colony on nearby Mandarte Island, British Columbia, only 5.0% (83 of 1,652) of sample eggs were lost or eaten in 1961–1962 (Vermeer 1963), and that 5.6% (26 of 466) of sample eggs were lost or eaten in 1979–1980 (Verbeek 1986). By comparison, during our 8 year study, more than a quarter of the sample eggs on Protection Island were lost or eaten, and more than a fifth of the total were cannibalized (Hayward et al. 2014). At a superficial level this suggests that the trends observed for ENSO fluctuations during 2006–2014 might be extrapolated to account for the effects of long-term warming. While this may be true, it is important to also note that Bald Eagle numbers have increased in the region, and that they now frequently prey on seabird eggs, chicks, and adults, given that populations of their more usual prey species have experienced dramatic declines (White et al. 2006, Hayward et al. 2010, Cowles et al. 2012, Hipfner et al. 2012, Henson et al. 2019). Thus, earlier Mandarte Island egg-loss numbers may be related in part to less eagle predation.

Using the effects of short-term SST fluctuations to shed light on the effects of long-term warming requires additional caution. For example, the average September–May SST in the water surrounding Protection Island prior to the 2016 breeding seasons equaled 10.02 °C (NOAA Port Townsend, Washington, buoy PTWW1), nearly 1 °C higher than during most years of our reproductive success–cannibalism study (Table 1). Contrary to expectation, however, few cannibal territories could be found in 2016 (JLH, pers. obs.), although no count was made. Conditions such as oxygen concentration, acidity, and temperature in the Salish Sea are heavily influenced by the intrusion of water from the adjacent Pacific Ocean (Irvine and Crawford 2013). Beginning in 2014 a mass of warm water called The Blob, independent of upwelling influenced by ENSO, accumulated in the North Pacific and persisted through the summer of 2016 (Kintisch 2015, Moore et al. 2016, Peterson et al. 2016a, 2016b). This occurrence seems to have led to complex ecosystem responses (Peterson et al. 2016a, 2016b), including ample food resources for the surface-feeding gulls on Protection Island (SMH and JLH, pers. obs.), yet also conditions associated with the starvation and death of deep-water-feeding Rhinoceros Auklets (*Cerorhinca monocerata*) in the region (S.F. Pearson, pers. comm.).

In summary, during years of higher SST, Glaucous-winged Gulls exhibited higher levels of egg cannibalism, higher levels of clutch-initiation synchrony, and longer and earlier clutch-initiation seasons than in years of lower SST. Clutch-initiation synchrony reduced the chance that a given egg was cannibalized. Short-term climate and resource fluctuations associated with ENSO events may select for behavioral plasticity in marine organisms, allowing long-lived individuals such as marine birds to switch between alternative life history tactics. The implications for long-term SST warming, however, remain unknown.

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