

## CONSTRAINTS ON CLUTCH SIZE IN THE GLAUCOUS-WINGED GULL

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**ABSTRACT.**—I examined three factors that may limit the clutch size of the Glaucous-winged Gull (*Larus glaucescens*) to three or fewer eggs: the energetic cost of egg formation, the shelf-life of eggs, and the incubation capacity of adults. Incubation capacity was found to have a significant effect on the success of large clutches but it cannot explain the absence of 4-egg clutches. Energetic limitation following the initiation of the clutch may be a more important factor limiting clutch size to three.

I examined several aspects of the brood reduction hypothesis to determine whether the presence of brood reduction adaptations is compatible with evidence that clutch size is not limited by the brood rearing capacity of the adults. Asynchronous hatching was found to be beneficial regardless of the number of young that could be raised and thus is consistent with evidence that brood-rearing capacity does not limit clutch size. The small size of the third egg, generally considered to be another brood reduction adaptation, was found to be a result of energetic shortages during laying and thus may not be an adaptive mechanism for brood reduction.

Members of the family Laridae exhibit modal clutch sizes ranging from 1 to 3 eggs, 4-egg clutches occurring infrequently (see Conover 1984). Some of the 4-egg clutches reported are produced by female-female pairs (Conover 1984). Clutch-size distributions with modal and maximal values of 3 eggs are found in at least 11 larid species: the Herring Gull (*Larus argentatus*), Laughing Gull (*L. atricilla*), Glaucous-winged Gull (*L. glaucescens*), Common Tern (*Sterna hirundo*), California Gull (*L. californicus*), Lesser Black-backed Gull (*L. fuscus*), Black-headed Gull (*L. ridibundus*), Common Gull (*L. canus*), Western Gull (*L. occidentalis*), Ring-billed Gull (*L. delawarensis*), and Great Black-headed Gull (*L. ichthyaetus*) (Samorodov and Ryabov 1969, Conover 1984). This group encompasses a diverse range of both body sizes and feeding habits, though most species are relatively large and all breed in temperate zones. The reason for the truncation of the clutch size frequency distribution at three eggs is not clear. Three factors—the energetics of egg formation, incubation capacity, and brood rearing capacity—have received attention as factors potentially limiting clutch size to three or fewer eggs.

The energetic cost of egg formation is thought to explain patterns of variation in larid egg size, clutch size, and nesting phenology (Nisbet 1973, 1977, Mills 1979, Pierotti 1982, Schreiber et al. 1979, Mills and Shaw 1980, Boersma and Ryder 1983, Houston et al. 1983, Winkler 1983, 1985, Pierotti and Bellrose 1986). The energetic cost of egg formation, however, does not place a strict upper limit on egg production at 3 eggs because protracted laying can be induced in at least 4 of the 11 species exhibiting a truncated clutch-size frequency distribution (Herring Gull: Paludan 1951, Harris 1964, Parsons 1976, Pierotti 1982;

Glaucous-winged Gull: this study; California Gull: Winkler 1983, 1985; Black-headed Gull: Weidmann 1956).

Similarly, the incubation capacity of gulls and terns may not impose a fixed upper limit on clutch size. Most large gulls have three brood patches (see Table 10) and it is possible that this brood-patch configuration results in a 3-egg limit (Vermeer 1963, Pierotti and Bellrose 1986). There are no studies, however, that support this hypothesis. Experimental manipulation of clutch size during incubation has shown that more chicks hatch from artificially enlarged clutches than from 3-egg clutches (Coulter 1973a, b).

There is also no evidence that clutch size is limited to 3 or fewer eggs by the brood-rearing capacity of the adults. In at least 4 species, adults are capable of rearing more than 3 young (Herring Gull: Haymes and Morris 1977; Glaucous-winged Gull: Vermeer 1963, Ward 1973; Lesser Black-backed Gull: Harris and Plumb 1965; Western Gull: Coulter 1973b).

To further complicate the question of clutch-size determination, many larids possess traits that potentially conflict with the observation that gulls are capable of raising more than 3 young. Two traits characteristic of all larids with 3-egg clutches are the presence of asynchronous hatching, and size reduction of the third (c-) egg relative to the first 2 (a- and b-) eggs. These traits are frequently cited as evidence supporting the brood reduction hypothesis (Lack 1968, O'Connor 1978, Clark and Wilson 1981, Hahn 1981, Slagsvold et al. 1984). Asynchronous hatching and the small size of the c-egg place the third chick at a disadvantage with respect to its siblings in competition for food. During years of food shortage, these traits are thought to facilitate the early mortality of chicks that could not be raised, thereby increasing food available to the surviving chicks. The presence of brood reduction traits is interpreted as circumstantial evidence that

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brood size is close to the limit set by food in years with high food availability (Lack 1968).

For two reasons, the presence of a brood reduction strategy may be compatible with the observation that gulls are capable of raising more than 3 chicks. First, those pairs capable of raising more than 3 chicks may not exhibit brood reduction adaptations. Second, even if all pairs do exhibit brood reduction adaptations, these adaptations are incompatible with the ability of the birds to raise more than 3 young only if they represent a cost during years when all young can be raised. For example, consider a pair that is capable of raising 4 young in a good year and 2 young in a bad year but lays a clutch of only 3 eggs. If the brood reduction strategy provides a benefit in bad years without reducing success in good years then there would be selection for the strategy regardless of the number of chicks that could be raised.

There is evidence, however, that brood reduction adaptations, particularly the small c-egg, do represent a cost in good years. The probability of chick survival was significantly correlated with egg size, controlling for order of laying, in the Common Tern (Nisbet 1973), the Herring Gull (Parsons 1970, 1975a) and the Black-headed Gull (Lundberg and Vaisanen 1979). Reduction in the size of the c-egg thus appears to reduce the probability of the survival of the third chick under any conditions. Consequently, the brood reduction strategy may conflict with evidence suggesting that clutch size is not limited during the chick stage.

In this paper I address two questions: first, why do Glaucous-winged Gulls have a modal clutch of 3, and second, why is the distribution truncated at 3 eggs. Because of evidence suggesting that clutch size is not limited by parental feeding ability, I focus on factors acting during laying and incubation that may limit clutch size to 3. In addition, because of the potential conflict between the presence of brood reduction adaptations and the assumption that clutch size is not limited during the chick period, I also examine the brood reduction hypothesis from the perspective of clutch size regulation.

I examined 3 factors potentially influencing the modal clutch size and the limitation of clutch size to 3 eggs. First, the energetic cost of egg formation could contribute to a 3-egg limit. Though in several species of gulls it has been demonstrated that females are capable of laying more than 3 eggs, the cost to the female of production of a fourth egg may be high enough that the net benefit of the egg is small. Second, the viability of unincubated eggs (shelf-life) may limit clutch size to 3. Most larids lay eggs at 2-day intervals and incubation does not begin until the

b-egg is laid. Since incubation begins prior to the completion of the clutch, the first 2 eggs hatch 1 or 2 days before the third. While it is generally assumed that asynchronous hatching, and thus the timing of the onset of incubation, are adaptations for unpredictable food resources, the same pattern could result if the timing of the onset of incubation was dictated by a short shelf-life of unincubated eggs. If early onset of incubation was required for egg survival this could limit clutch size to 3 since a fourth chick would hatch nearly 4 days after the first and thus be at an extreme competitive disadvantage. Finally, the incubation capacity of adults places a proximate limit on the number of eggs that can be hatched. I evaluated the role of incubation capacity as a constraint on clutch size by measuring the hatching success of artificially enlarged clutches.

I examined 3 aspects of the brood reduction hypothesis to determine whether it conflicted with the assumption that clutch size is not limited during the chick-rearing stage. First, the conflict would be avoided if some pairs did not show evidence of brood reduction adaptations. I measured the natural patterns of hatching synchrony and c-egg size to determine whether the survival probability of chicks was equalized in some broods through synchronous hatching and uniform egg size. Second, I examined the costs and benefits of asynchronous hatching to determine whether predictions of the brood reduction hypothesis are met and to determine whether asynchronous hatching represents a cost under conditions where 3 or more young can be fledged. Finally, I tested the role of energetic limitations as an alternative explanation for the small c-egg. The reduced c-egg size appears to represent a cost to the adults under circumstances when 3 or more young can be fledged. If, however, the small size of this egg is not an adaptation for brood reduction, then it would be compatible with the assumption that clutch size is not limited during the chick period.

## METHODS

### GENERAL

This study was conducted on Protection Island, Washington (48°07'N, 122°55'W) between May and August of 1983–1985. All experiments were carried out on a 700 × 100-m sandspit which is used by roughly 5000 pairs of breeding gulls. Vegetation on the spit ranges from bare ground to 1.5-m tall grass (*Elymus mollis*). Chicks are fed almost exclusively fish, primarily sandlance (*Ammodytes hexapterus*) and herring (*Clupea harengus*), but adults forage both on natural food sources and at garbage dumps (10 to 25 km from the colony) throughout the breeding season.

In several experiments, I made use of data collected at 250 nests which had been monitored since 1983. At least one adult at each nest was color-banded. The

banded adults were nest-trapped during incubation (see Amlaner et al. 1978), weighed, and measured (tarsus, culmen, bill depth, bill width, wing chord, radius, body length). Sex was determined for 83 birds by the observation of copulations, and for the remainder of the birds through the use of a discriminant function created for the birds of known sex (98.9% accuracy for birds of known sex). Weights and measurements of birds were log-transformed prior to all analyses.

All experiments were performed at nests sampled randomly with respect to the time of laying. Nests utilized in the study were marked and assigned to experimental groups prior to laying. The age of adults is known to influence laying phenology and clutch size in several larid species (Coulson 1963, Davis 1975, Coulson and Horobin 1976, Mills 1979, Mills and Shaw 1980). The ages of adults in experimental groups in this study represent a random sample of the birds present.

All significance tests are one-tailed unless otherwise noted.

#### ENERGETIC REQUIREMENTS

##### *Food supplement*

Forty nest scrapes or obvious territories in an area of dense vegetation were marked on 7 May 1985. On 23 days between 8 May and 5 June, approximately 200 g (dry weight) of a moistened mixture of Purina Cat Chow and Darigold Cat Food was placed beside odd numbered nests with even numbered nests serving as controls. The experiment was conducted in tall grass in order to minimize disturbance by crows. The food was placed in small containers and these were partially concealed in the grass adjacent to the nest scrape. Food was provided at each nest until the laying date of the a-egg. No eggs were laid at 8 marked territories, leaving a sample of 18 experimental and 14 control nests. Nests were checked daily until 22 May (date of first clutch initiation) and twice daily subsequently. I was absent from the island on two occasions for 3- and 4-day periods; laying dates during these periods were estimated to be 48 h prior to the laying of the b-egg (Vermeer 1963). Egg length and breadth were measured to the nearest 0.1 mm and the eggs were weighed to the nearest 0.5 g.

At an additional seven nests I provided food to pairs in which the females had been color-banded and for which I had obtained information on egg size and laying date in 1984. Other nests with marked females served as controls for these 7 pairs. For comparisons between these groups I used egg volumes calculated using the formula: volume =  $0.476 \times \text{length} \times \text{breadth}$ .<sup>2</sup>

It was not possible to observe whether birds in the 40-nest grid ate the supplemental food. All birds at the 7 nests with banded birds were seen to eat the food, some within seconds of my departure from the territory.

##### *Egg removal*

At 16 of the nests in the 40-nest feeding grid and at additional 34 nests with 1 or more color-banded adults, I removed the a-egg within 12 h of laying in order to stimulate production of a fourth (d-) egg.

#### SHELF-LIFE

Between 25 May and 13 June 1985, I collected the first egg from 113 clutches within 12 h of laying, marked each egg with the date (written on tape), and placed each in an artificial nest, composed of the lining of several nests, which I shaded and fenced to exclude predators. Air temperatures during this period ranged from 4–26°C. After leaving each egg unincubated for 0–8 days (2-day intervals) I substituted 2 or 3 of these experimental eggs for eggs in 34 clutches at marked nests which had been completed within the previous 24 h. The 34 nests were checked daily during hatching and the success of each egg was recorded.

#### INCUBATION CAPACITY

Between 25 May and 13 June 1985, I manipulated the clutch size of 89 completed nests by adding or removing between 1 and 3 eggs. Manipulations were done within 4 days of clutch completion and eggs that were added to nests were of the same age as the eggs already present in the nest. I did not switch eggs between control clutches of 3 eggs. All nests were checked daily during hatching and hatching success was recorded.

#### SIZE OF C-EGG

Between 25 May and 13 June 1985, supplemental food was provided (as above) to 31 nests within 24 h of the laying of the a-egg and on each of the subsequent 4 to 5 days. Twelve nests were excluded from the analysis because of egg loss prior to weighing ( $n = 6$ ) or because the completed clutch contained fewer than 3 eggs ( $n = 6$ ). Each egg was measured and weighed within 48 h of laying. Eggs of known laying sequence in the remainder of the colony served as controls.

To examine patterns of attendance at the nest during and prior to incubation, I observed 87 nests from 3 elevated (2 m) wooden blinds. I conducted 15 3-h watches between 24 May and 30 June 1985. Each nest was observed on an average of 3.6 occasions. At 10-min intervals I scanned all nests visible from the blind and recorded the presence or absence of each member of the pair. At all but 8 of the nests at least 1 bird was color-banded. The importance of time budget information on the day of laying of the a-egg was recognized late in the season and so the 8 unbanded pairs, without eggs, were chosen and followed through egg laying. The median laying date for nests observed during the laying of the first egg (14 June) was later than for the colony as a whole (3 June), and there is a potential that this may have introduced some variance into the measured attendance patterns. I report attendance patterns only in terms of the amount of time both members of the pair were present since this removes the potential error of misidentification of the bird.

#### HATCHING SYNCHRONY

##### *Natural pattern*

Fifty-four nests, chosen randomly from the entire sample of 300 nests followed in 1985, were checked twice daily at the time of hatching to determine the time span between the hatching of the first and third chick. The order of laying was not known for all eggs so I could not calculate the relative size of the c-egg. Instead, I calculated the ratio of the smallest to largest

TABLE 1  
CLUTCH SIZE DISTRIBUTIONS OF NESTS WITH AND WITHOUT SUPPLEMENTAL FOOD PRIOR TO LAYING

Group	Food supplement	Number of eggs laid				Total nests
		1	2	3	4	
First egg not removed						
Experimental	Yes	0	2	6	0	8
Control	No	0	2	6	0	8
First egg removed						
Experimental	Yes	2 <sup>a</sup>	2	4	2	10
Control	No	0	1	4	1	6
Banded control	No	1 <sup>a</sup>	3	13	17	34

<sup>a</sup> Nests abandoned after removal of egg.

egg in each clutch as a measure of the size range of eggs; this ratio should estimate the relative size of the c-egg.

#### Manipulations

Between 25 May and 13 June 1985, hatching synchrony was manipulated at 46 nests within 10 days of clutch completion. Under normal conditions, the third chick hatches 30 h after the second (see below). At 22 "synchronous" nests the c-egg was exchanged with a c-egg laid 1 day previously to create clutches in which the b- and c-eggs hatched synchronously. At 24 "asynchronous" nests the a-egg was exchanged with an a-egg laid 2 days previously to create a pattern of hatching that would result if incubation began on the day of clutch initiation. Another 31 nests that hatched all 3 chicks were not manipulated and served as controls. For several reasons (egg death, predation, and chick death prior to the hatching of all 3 chicks), only 11 of the synchronous and 9 of the asynchronous nests in the original design could be used in the experiment. Consequently, I created 32 additional experimental broods by adding 1 newly hatched (wet) chick to each of 5 of the original synchronous nests and 11 of the asynchronous nests that had lost 1 egg, and by replacing young chicks (less than 3 day old) at 16 other nests with 3 newly hatched chicks. The hatching order of the chicks added to these nests was not known. Results from the entire sample of nests matched the results from nests in the original study design and in the following analysis only the results for the entire sample

of 32 synchronous and 20 asynchronous nests are reported.

Chicks at each nest were individually marked with tape bands on hatching and banded with aluminum bands on day 20. At approximately day 0, 10, 20, and 35 the chicks were weighed and the tarsus, culmen, and (on day 20 and 35) wing chord were measured. Weights and measurements were log-transformed prior to analysis. Chicks that were seen after day 32 are assumed to have fledged (fledging does not actually occur until approximately day 40). Sixty of 85 chicks that did not fledge were found dead and the age of death was estimated to the nearest day. The remainder of the chicks are presumed to have died and age of death was taken to be the age when last observed (19 of the 25 were not found at the 10-day check).

Growth rates were compared by testing for size differences at age 20 and 35. Two measures of size were used: chick weight, and a principal component factor score ("chick size") combining all measurements. Because of the substantial variation in chick weight resulting from periodic feedings, body size measurements are preferable indicators of growth. Principal components analysis allows the incorporation of several measurements of the size of the chick into 1 score reflecting overall size. Separate principal components analyses were performed for chicks of age 17–24 and age 32–37. Loadings on PCI at age 20 were: culmen .87, tarsus .89, weight .95, wing .86; and at age 35: culmen .83, tarsus .83, weight .96, wing .79. Not all chicks were measured at exactly ages 20 and 35. I adjusted the measured weights and sizes to these ages using the slopes of regressions of weight and size on age for the 2 intervals of 17–24 days and 32–37 days. Mean chick weights and chick sizes were then calculated for each nest (to avoid violation of the assumption of independence of measurements).

## RESULTS

### ENERGETIC REQUIREMENTS

#### Timing of laying

There was no significant difference in the timing of clutch initiation between food supplemented ( $n = 18$ ) and control nests ( $n = 14$ ) (median laying dates were 2 June and 3 June respectively; Mann-Whitney U,  $P > .10$ ). Food had been provided for 13 days prior to the initiation of the first clutch (22 May). The seven

TABLE 2  
FACTORS INFLUENCING THE TENDENCY FOR BIRDS TO LAY A FOURTH EGG FOLLOWING REMOVAL OF THE FIRST EGG: MEAN  $\pm$  SD (N)

Factor	Number of eggs laid		Significance*
	Three or fewer	Four	
Weight of a-egg	96.2 $\pm$ 6.6 (16)	93.0 $\pm$ 8.1 (16)	.21
Laying date of a-egg (days after 1 May 1985)	34.2 $\pm$ 4.7 (17)	31.2 $\pm$ 4.2 (16)	.04

\* Two-tailed Mann-Whitney U.

TABLE 3  
SHELF LIFE OF UNINCUBATED EGGS

	Days without incubation				
	0	2	4	6	8
Initial number of eggs	23	22	24	21	23
Total hatching (%)	20 (87)	20 (91)	17 (71)	17 (81)	16 (70)
Total lost during incubation	2	0	5	3	4
Percent success of eggs not lost	95	91	89	94	84

food supplemented nests with banded females initiated clutches 2.7 (SD = 2.1) days earlier in 1985 than in 1984; 71 control nests initiated clutches 1.9 (SD = 6.7) days earlier (Mann-Whitney U,  $P > .20$ ).

#### Egg size

There was no difference in the weight of the a-egg between food supplemented (95.7 g, SD = 6.2,  $n = 18$ ) and control nests (95.0 g, SD = 8.6,  $n = 14$ ) in the 40-nest grid ( $t = .26$ ,  $P > .25$ ). There was also no difference in a-egg weight between all supplemented nests (96.4 g, SD = 7.1,  $n = 25$ ) and 131 nests in the remainder of the colony for which I had accurate weights of the a-egg (95.0 g, SD = 7.8) ( $t = .87$ ,  $P > .10$ ). There was no difference in the change in total clutch volume between 1984 and 1985 when the 7 supplemented nests with records of egg size in 1984 were compared to 71 control nests (supplemented: +1.85 cc, SD = 2.01; control: +.89 cc, SD = 3.73; Mann-Whitney U,  $P > .10$ ).

#### Egg removals

A fourth egg was laid in 40% of nests from which the first egg was removed (Table 1). There was no indication that birds at nests which had received supplemental food were more likely to lay a fourth egg. Pairs in the 40-nest feeding grid

(food supplemented and control combined) were less likely to produce a d-egg than pairs at the 32 nests with banded birds ( $G = 4.72$ ,  $df = 1$ ,  $P < .05$ ). The reason for this difference is not clear, though it may be due to the greater disturbance caused by my regular feeding visits to the 40-nest grid.

If female condition influences the ability to lay a d-egg, then it would be predicted that females laying large eggs would be more likely to lay a d-egg. There was no relationship between the size of the a-egg and the tendency to lay a d-egg (Table 2). Birds that laid a d-egg, however, initiated clutches on average 3 days earlier than those that did not (Table 2).

#### SHELF-LIFE

Twenty-four of the 113 eggs involved in the shelf-life experiment did not survive to hatch. Hatching success was not affected by the amount of time that the eggs were unincubated (Table 3;  $G = 5.28$ ,  $P > .25$ ). Thirteen of the eggs that did not survive were lost from the nest prior to hatching. I also examined the hatching success of only those eggs that were present in the nest after the standard incubation period and again there were no differences among groups (Table 3;  $G = 2.49$ ,  $P > .50$ ).

TABLE 4  
EFFECT OF CLUTCH SIZE ON HATCHING SUCCESS<sup>a</sup>

	Clutch size				
	1	2	3	4	5
Number of nests	18	14	19	20	18
Number of eggs	18	28	57	80	90
Eggs developed (%)	13 (72)	24 (86)	<u>51 (89)</u>	49 (61)	60 (67)
Eggs hatched (%)	13 (72)	24 (86)	<u>50 (88)</u>	47 (59)	48 (53)
Eggs developed per nest	.72	1.71	2.68	2.45	<u>3.33</u>
Egg hatched per nest	.72	1.71	<u>2.63</u>	2.35	<u>2.67</u>
Number of nests hatching one or more (%)	13 (72)	13 (93)	<u>19 (100)</u>	16 (80)	13 (72)

<sup>a</sup> Highest value underlined.

TABLE 5  
VOLUME (cc) OF EGGS OF THE GLAUCOUS-WINGED GULL BY SEQUENCE OF LAYING: MEAN  $\pm$  SD (N)<sup>a</sup>

Year	Egg order		
	First	Second	Third
<b>Three-egg clutches</b>			
1983	86.35 $\pm$ 6.22 (89)	85.41 $\pm$ 6.19 (62)	79.79 $\pm$ 5.97** (82)
1984	84.79 $\pm$ 6.66 (88)	83.34 $\pm$ 6.81 (47)	77.52 $\pm$ 6.76** (92)
1985	85.96 $\pm$ 7.49 (72)	84.64 $\pm$ 8.14 (43)	79.75 $\pm$ 7.18** (73)
Combined	85.69 $\pm$ 6.77 (249)	84.64 $\pm$ 6.99 (152)	78.93 $\pm$ 6.70** (247)
<b>Two-egg clutches</b>			
1983	83.95 $\pm$ 6.71 (20)	82.64 $\pm$ 7.39 (18)	
1984	84.63 $\pm$ 8.17 (30)	81.37 $\pm$ 7.36 (29)	
1985	84.59 $\pm$ 5.91 (48)	81.20 $\pm$ 5.86* (35)	
Combined	84.47 $\pm$ 6.77 (98)	81.58 $\pm$ 6.70* (82)	

<sup>a</sup> Difference between each egg and the first egg is tested.

\*  $P < .05$ , two-tailed t-test.

\*\*  $P < .001$ .

#### INCUBATION CAPACITY

Hatching success differed significantly among clutches of different size (Table 4;  $G = 28.0$ ,  $df = 4$ ,  $P < .001$ ). Peak hatching success (88%) was found for clutches of 3 eggs, and success fell rapidly in larger clutches. Part of the decline in hatching success in large clutches could be attributed to the tendency for pairs to stop incubation of viable (and sometimes pipped) eggs after 3 or 4 chicks had hatched. Consequently I also present results for 'development success', that is, the percent of eggs for each clutch size which developed to the point of pipping.

The average number of eggs hatched per nest was highest for clutches of 3 and 5 eggs; however, differences among clutches of 3 or more eggs were not significant (Kruskal-Wallis ANOVA,  $P =$

.54). The average number of developed eggs per nest differed significantly among clutches of 3 or more eggs (Kruskal-Wallis,  $P = .05$ ). The number of developed eggs per nest was significantly higher in clutches of 5 than in clutches of 3 eggs (Mann-Whitney U, two-tailed  $P = .04$ ). The probability of hatching at least 1 chick was highest in clutches of 3.

#### SIZE OF THE C-EGG

In each of the 3 years of this study the c-egg was significantly smaller than the a-egg (Table 5). In 2-egg clutches the b-egg was smaller than the a-egg only in 1985. Food supplementation provided on the day of laying of the a-egg resulted in an increase in the size of the c-egg (Table 6). The size of the c-egg in supplemented nests did

TABLE 6  
EFFECT OF FOOD SUPPLEMENTATION ON THE WEIGHT OF THE C-EGG: MEAN (G)  $\pm$  SD (N)<sup>a</sup>

	Egg order		
	First	Second	Third
Control	95.74 $\pm$ 8.27 (72)	94.56 $\pm$ 8.89 (43)	89.15 $\pm$ 8.23 (71)
Food supplement	94.95 $\pm$ 6.48 (19)	95.39 $\pm$ 7.46 (19)	93.06 $\pm$ 8.54* (18) <sup>b</sup>

<sup>a</sup> Differences between eggs of same order in laying sequence are tested.

<sup>b</sup> One egg was broken.

\*  $P < .05$ , one-tailed t-test.

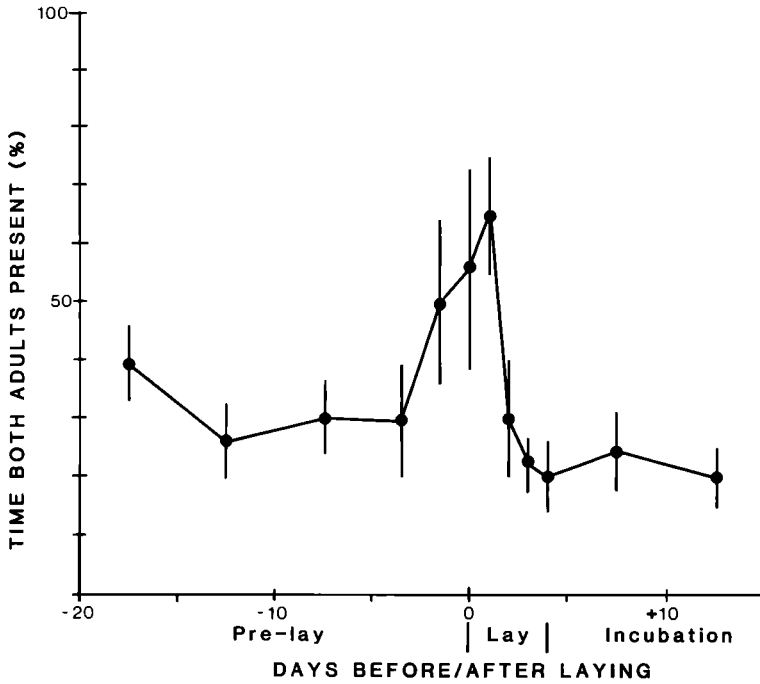


FIGURE 1. Percent of time during which both adults were present on territory as a function of days before and after laying of a-egg (Day 0). Means calculated from an average of 19.3 different nests (9.9 nests between -4 and +4 days). Mean  $\pm$  SE.

not differ from the size of the a-egg ( $t = .75, P > .10$ ; a difference less than 4.23 g could not be detected with this test).

The amount of time during which both members of a pair were on territory increased immediately prior to the initiation of laying and declined thereafter (Fig. 1).

SYNCHRONY

At 54 nests that were checked twice daily, the third chick hatched 41.2 h ( $SD = 16.8$ , range 12–72 h,  $n = 54$ ) after the first chick. The second chick hatched 9.7 h ( $SD = 9.1$ , range 0 to 36 h,  $n = 48$ ) after the first. There was a significant positive correlation between the date of hatching and the length of time between the hatching of the first and third chicks ( $r = .27, P = .03$ , Spearman rank), but not with either egg size ( $r = -.01, P > .40$ ) or the range of egg sizes in the clutch ( $r = -.01, P > .40$ ).

Among nests used in the experimental study of synchrony (checked daily during hatching) the interval between hatching of first and third chicks was 9.4 h for synchronous ( $SD = 17.3$ , range: 0–48 h,  $n = 32$ ), 39.1 h for control ( $SD = 15.1$ , range: 0–48 h,  $n = 31$ ), and 88.8 h for asynchronous nests ( $SD = 25.9$ , range: 48–144 h,  $n = 20$ ).

There were no significant differences in the

number of chicks raised to day 35 between the experimental groups (Table 7; G-tests between each pair,  $P > .25$ ). The success of asynchronous nests, however, is artificially inflated because I did not include nests that failed to hatch all 3 chicks. At 4 of these nests, the adults ceased incubation of otherwise viable eggs when the first chick was 6 days old. Moreover, the most successful asynchronous nests tended to be those with the least hatching asynchrony, though the pattern was not significant.

Chicks that died, in both control and asynchronous broods, died at younger ages than chicks in synchronous broods (Fig. 2; median age: synchronous—day 12, control—day 7.5, asynchron-

TABLE 7  
CHICKS RAISED TO 35 DAYS FROM BROODS WITH MANIPULATED SYNCHRONY

	Number of nests	Number of chicks fledged				Mean $\pm$ SD
		0	1	2	3	
Synchronous	32	3	6	14	9	1.91 $\pm$ .93
Control	31	3	5	13	10	1.97 $\pm$ .95
Asynchronous	20	2	4	5	9	2.05 $\pm$ 1.05 <sup>a</sup>

<sup>a</sup> Artificially inflated (see text).

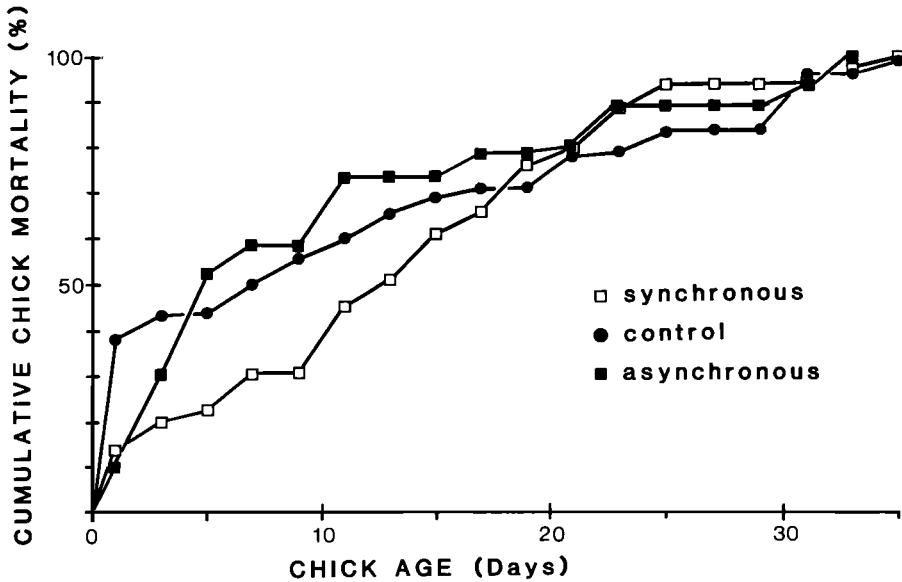


FIGURE 2. Cumulative percent mortality of chicks as a function of chick age. Sample size: synchronous, n = 35; control, n = 32; asynchronous, n = 19 chicks.

ous—day 5). The distribution of age at death differed significantly between synchronous and control broods (Kolmogorov-Smirnov,  $D = .248$ ,  $n = 32$ ,  $P < .05$ ), and approached significance between synchronous and asynchronous broods (K-S,  $D = .298$ ,  $n = 19$ ,  $P = .06$ ). In all groups, over 60% of the chick mortality occurred by day 15.

The predicted advantage of a brood reduction strategy is that the early death of a chick that cannot be raised to fledging will result in more rapid growth of the remaining offspring. Thus, growth rates, in broods from which 2 chicks fledged, should be higher in control than in synchronous broods due to the earlier mortality among third-hatched control chicks. I compared

the growth rates of chicks which subsequently fledged, among broods which fledged 2 chicks. Chick size and weight on day 20, but not on day 35, was significantly lower in synchronous broods (Table 8). There was a significant negative correlation between age of chick death and the size of surviving chicks on day 35 (Fig. 3).

In the context of the brood reduction hypothesis it is generally assumed that there is no advantage to asynchrony in broods where all 3 young can be raised; that is, the advantage should only be found in broods in which 2 chicks survive. In this experiment, however, the chick size and weight in nests from which all 3 chicks fledged, was significantly lower in synchronous nests than in controls on both day 20 and 35 (Table 9).

TABLE 8  
GROWTH RATES OF CHICKS IN BROODS FROM WHICH TWO CHICKS FLEDGED<sup>a</sup>: MEAN  $\pm$  SD (NUMBER OF NESTS)

Experimental group	Age 20		Age 35	
	Weight (g)	Signif. wt/size <sup>b</sup>	Weight (g)	Signif. wt/size
Synchronous	564 $\pm$ 140* (13)	.05/.03	895 $\pm$ 287 (3)	.15/.19
Control	637 $\pm$ 62 (13)		935 $\pm$ 84 (9)	
Asynchronous	571 $\pm$ 49* (4)	.03/.08	912 $\pm$ 67 (2)	.46/.39

<sup>a</sup> Raw data represents the average, for each nest, of the weight/size of chicks that survived to fledge. Weight/size was adjusted to the ages of 20 and 35. Differences from control nests are tested. All statistics were done on log transformed weights. Asymmetry resulting from the transformation of the standard deviation back to grams was averaged.

<sup>b</sup> One-tailed Mann-Whitney U.

\*  $P < .05$ .



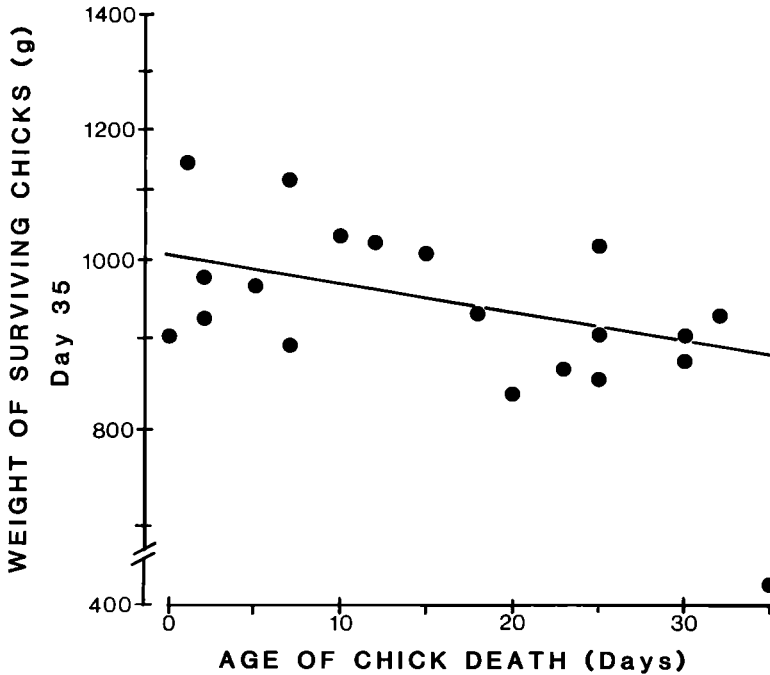


FIGURE 3. Average weight (g) at day 35 of surviving chicks ( $\text{Log}_{10}$  scale), in broods from which two chicks fledged, as a function of the age of death of the chick that died. Regression line excludes outlier. (Weight: Spearman rank  $r = -.39$ ,  $P = .05$ ,  $n = 19$  excluding outlier;  $P = .02$  including outlier; Size:  $r = -.42$ ,  $P = .04$ ,  $n = 19$  excluding outlier;  $P = .01$  including outlier).

DISCUSSION

CLUTCH-SIZE REGULATION

Two factors, incubation capacity and food limitation following the initiation of laying, could limit clutch size in the Glaucous-winged Gull. The shelf-life of eggs and the energetic cost of egg formation during the pre-laying period appeared to have little effect on clutch size.

Pre-laying energetics has received considerable attention as a factor influencing larid clutch size (Bateson and Plowright 1959, Lack 1968,

Coulson and Horobin 1976, Nisbet 1977, Winkler 1983, 1985). Houston et al. (1983) have shown that the protein reserves of female Lesser Black-backed Gulls are correlated with both potential clutch size and egg weight. A connection between body condition and the timing of laying has been shown in the Ring-billed Gull (Boersma and Ryder 1983). Nisbet (1973, 1977) found that the amount of courtship feeding by Common Terns was correlated with subsequent total clutch weight and the weight of the c-egg and also found a correlation between female body weight at the

TABLE 9  
GROWTH RATES OF CHICKS IN BROODS FROM WHICH THREE CHICKS FLEDGED<sup>a</sup>: MEAN  $\pm$  SD (NUMBER OF NESTS)

Experimental group	Age 20		Age 35	
	Weight (g)	Signif. wt/size <sup>b</sup>	Weight (g)	Signif. wt/size
Synchronous	594 $\pm$ 124* (9)	.01/.01	910 $\pm$ 118* (3)	.02/.01
Control	708 $\pm$ 77 (9)		1037 $\pm$ 84 (8)	
Asynchronous	574 $\pm$ 60* (9)	.003/.005	931 $\pm$ 79* (8)	.03/.01

<sup>a</sup> Raw data represents the average, for each nest, of the weight/size of the three chicks. Weight/size was adjusted to the ages of 20 and 35. Differences from control nests are tested. All statistics were done on log-transformed weights. Asymmetry resulting from the transformation of the standard deviation back to grams was averaged.

<sup>b</sup> Two-tailed Mann-Whitney U.

\*  $P < .05$ .

TABLE 10  
NUMBER OF BROOD PATCHES AS RELATED TO CLUTCH SIZE FREQUENCIES<sup>a</sup>

Species	Clutch size frequency (%)				Ave. clutch	N	Brood patches	Reference
	1	2	3	4				
Fairy Tern <i>Gygis alba</i>	100				1.00	213	1	Dorward 1963
Swallow-tailed Gull <i>Creagrus furcatus</i>	100	*			1.00	>2000	2	Harris 1970
Royal Tern <i>Sterna maxima</i>	98.6	1.4			1.01	911	2	Buckley and Buckley 1972
Grey Gull <i>Larus modestus</i>	46.7	51.6	1.6		1.55	182	2	Howell et al. 1974
Ivory Gull <i>Pagophila eburnea</i>	31.2	68.7	*		1.69	32	3	Bateson and Plowright 1959
Kelp Gull <i>L. dominicanus</i>	19	76	5		1.86	21	3	Williams et al. 1984
California Gull <i>L. californicus</i>	7.0	44.2	48.8		2.42	43	3	Unpub. data <sup>b</sup>
Common Tern <i>S. hirundo</i>	20.4	65.0	14.3	0.2	1.94	2032	3	Winkler 1983, Johnston 1956
Glaucous-winged Gull <i>L. glaucescens</i>	7.7	23.4	68.0	0.8	2.62	951	3	Conover 1984 <sup>c</sup> , Gochfeld 1977
Black-headed Gull <i>L. ridibundus</i>	2.7	21.2	76.1		2.73	704	3	This study
Laughing Gull <i>L. atricilla</i>	4.6	14.1	80.7	0.5	2.77	1217	3	Conover 1984 <sup>c</sup> , Beer 1961
Herring Gull <i>L. argentatus</i>		18.0	82.0		2.82	111	3	Dinsmore and Schreiber 1974
	2.5	6.9	90.6		2.88	160	3	Drent 1970

<sup>a</sup> Data on clutch size is taken from same source as data on brood patch number where possible (same locality for California Gull).

<sup>b</sup> Punta Tombo, Argentina, November 1983.

<sup>c</sup> Post-1950 data only.

\* Rare.

initiation of laying and clutch size. Energetic limitations may also provide an explanation for the reduced clutch size of the California Gull at Mono Lake (Winkler 1983, 1985).

There are several potential explanations for the absence of any apparent effect of supplemental food during the pre-laying period on egg size, laying date, or potential clutch size, in this study. First, the Glaucous-winged Gull is larger than other larids in which pre-laying energetics have been examined. The greater body size may serve to buffer the Glaucous-winged Gull from energetic factors immediately prior to laying. Second, food was provided for only 24 days prior to the median laying date of the a-egg and this may not have been sufficient time to have an effect. In other species (mostly passerines), significant advances in laying date have resulted when food was provided for 25–200 days prior to the mean laying date of controls (Ewald and Rohwer 1982). Finally, because of variation in the number of follicles that begin enlargement (Houston et al. 1983), increased energetic resources could result in the enlargement of a greater number of ova rather than increased allocation to each egg. In this case, however, the food-supplemented birds should have been more likely to lay a fourth egg; this was not observed. Spaans

(cited in Drent and Daan 1980) reportedly found an advancement in laying date in Herring Gulls provided with supplemental food but there appear to be no other experimental data for the Laridae. Parsons (1976) argued that pre-laying energetics does not affect laying date in gulls based on the evidence that early nesting birds lay the largest eggs.

Supplemental food is known to affect breeding patterns in several other species of birds (Ewald and Rohwer 1982), although this is not always the case. Poole (1985) failed to find an effect of supplemental food on laying date or egg size in the Osprey (*Pandion haliaetus*) and Niebuhr (1981) found no correlation between courtship feeding and laying date in the Herring Gull. Food supplementation may not increase energetic resources available to the female but may instead substitute for courtship feeding and foraging. Food provided to incubating Herring Gulls results in an increase in time spent on territory (Shaffery et al. 1985). If benefit of increased egg size or earlier nesting is less than the benefit of territorial presence prior to laying, then increased energetic resources may be directed to the latter use.

Both this study and that of Parsons (1976) have found a correlation between laying date and

the ability to produce a d-egg. This correlation is consistent with an energetic explanation if earlier breeders are in better condition (Boersma and Ryder 1983); however, this pattern could also result if, among late breeders, the advantage of earlier hatching exceeds the advantage of a third egg. Parsons (1976) found that birds that laid more than 3 eggs tended to lay larger first eggs. This pattern was not observed in this study, possibly because egg size does not appear to be correlated with laying date on Protection Island.

Incubation capacity may play a role in the regulation of clutch size in the Glaucous-winged Gull but its relative importance is questionable. More than 3 chicks can be hatched from artificially enlarged clutches, though hatching success per egg declines sharply among enlarged clutches. Because this study and that of Coulter (1973a, b) are indicative only of the proximate effect of incubation capacity on clutch size determination, its role as an ultimate constraint on clutch size is even more questionable.

There are 3 groups of birds in which incubation capacity has been a prominent hypothesis in the explanation of patterns of clutch size frequencies: the Charadrii (shorebirds), the Stercorariidae (jaegers and skuas) and the Laridae (Lack 1947, Klomp 1970, Andersson 1976, Winkler and Walters 1983). Some of the species in each group exhibit a truncated clutch size distribution, and yet have been shown to have the energetic resources necessary for production of extra eggs and the ability to fledge extra young. The incubation capacity hypothesis seems most plausible in the shorebirds, where the extremely large egg size, relative to body size, may place a physical limit on the number of eggs that can be incubated. Even here, though, experimental evidence for limits imposed by incubation capacity is not conclusive (Shipley 1984). In the Laridae and Stercorariidae the argument for incubation capacity as an ultimate limitation must rely on genetic, physiological, and developmental constraints since other species of similar size are capable of incubating larger clutches (Rohwer 1985, Fredrickson 1969).

There are 2 arguments against incubation capacity as an ultimate limitation to clutch size in the Laridae. First, over evolutionary time, the number of brood patches appears to be a plastic trait (Table 10). Species with small average clutch size have fewer brood patches. Since loss of a trait is easier than evolution of a novel trait, this evidence of plasticity is weakened if the primitive condition was to have 3 brood patches (e.g., Lack 1968). Second, there may be mechanisms other than the evolution of a 4th brood patch (3rd in the case of the Stercorariidae) that would allow efficient incubation of extra eggs. Increased

heat transfer to the eggs, coupled with more frequent movement of eggs in the nest, is one such mechanism. Boersma and Ryder (1983) have documented variability in the vascularization of brood patches in incubating Ring-billed Gulls and this could potentially have a genetic basis. Enlargement of existing brood patches could also increase incubation efficiency. Drent (1970) found variability in brood patch size in incubating gulls; however, this may be attributed, at least in part, to differences in stage of incubation (F. Pitelka, pers. comm.). Because of the large egg size, a substantial increase in brood patch size would be necessary before 2 eggs could be incubated with a single brood patch.

In both this study and Coulter's (1973a, b), the benefit of more than 3 eggs, in terms of number of chicks hatched, was small. Thus, cost to adults of the production of a 4th egg would have to be small for a 4-egg clutch to result in a net benefit. In addition, I found that probability of loss of the entire clutch increased among enlarged clutches. Increased risk of a complete breeding failure may exceed the benefit of a 4th egg.

Mean hatching success may not be the most appropriate measure of the constraint imposed by incubation capacity. In 3 of the 20 4-egg clutches (15%) and 3 of the 18 5-egg clutches (17%), the entire clutch was successfully hatched. Existing variability in incubation behavior and physiology would seem to allow "good" pairs to lay extra eggs and successfully incubate them. Thus, incubation capacity does not impose a strict limit on clutch size, though it clearly decreases the marginal benefit of extra eggs.

In this study, the size of the c-egg was shown to be influenced by the amount of food available to the female following clutch initiation. There are currently 5 hypotheses that could account for the small size of the c-egg in gulls and terns. Three explanations assume that the reduced size of the c-egg is adaptive. Evidence for this assumption appears to be strong since the c-egg does not show a reduction in size following the removal of the a-egg, while the d-egg (if laid) is reduced in size (Paludan 1951, Parsons 1976). The female thus appears to have the energetic resources necessary to produce a large c-egg. First, the reduced size of the c-egg has been considered to be an adaptation for brood reduction (O'Connor 1978, Clark and Wilson 1981, Hahn 1981, Slagsvold et al. 1981). Clark and Wilson (1981) single out the small c-egg of gulls and terns as the only example of reduced egg size in which it appears that the reduction in size is an adaptation to impair the competitive ability of an offspring.

Second, Graves et al. (1984) argue that the c-egg represents an insurance egg only, hence the egg size is of little importance relative to ener-

getic costs and time constraints. This explanation cannot suffice for all species which exhibit this trait since many populations frequently fledge three young (e.g., this study).

Finally, Parsons (1972, 1976) found that the length of incubation of the c-egg was relatively short and suggested that the small size functions to increase hatching synchrony, particularly when egg predation forces the early onset of incubation. There is no reason, however, to believe that gulls could not effectively guard eggs without transferring heat to them and thus it seems unlikely that predation rates could force asynchrony unless the probability of egg predation remained high even after the clutch was completed (Clark and Wilson 1981).

There have been 2 maladaptive explanations for the small size of the c-egg. First, Paludan (1951) suggested that the small size of the c-egg is simply a physiological response to the onset of incubation. Since other species of birds are capable of laying large last eggs after the onset of incubation (Clark and Wilson 1981), this argument has little support.

Second, Houston et al. (1983) have argued that the small c-egg is a result of a reduction in protein intake by the female after the onset of laying. A small c-egg has been found in every larid species investigated with the exception of the Black Tern (*Chlidonias niger*) and 1 population of the Western Gull (Pierotti and Bellrose 1986) (Table 11). The c-egg is characterized by the possession of the same amount of yolk but less albumen than the a- and b-eggs (Parsons 1976, Houston et al. 1983). Houston et al. (1983) found no correlation between female protein or lipid reserves and albumen weight and suggested that protein for albumen is derived from food intake between ovulation and laying (see Jones and Ward 1976). They suggest that the c-egg size is reduced because the female has less time available to forage after the onset of laying. Houston et al. (1983) cite the finding of a correlation between the extent of courtship feeding in Common Terns and the weight of the c-egg (Nisbet 1973) as evidence in support of this hypothesis. I calculated the weight of the c-egg relative to the average weight of the first 2 eggs from the data Nisbet (1973) presented and found no correlation ( $r = .09$ ,  $P > .25$ , Spearman rank) between relative c-egg size and courtship feeding. The correlation between courtship feeding and third egg size was largely due to the strong correlation between total clutch weight and the size of the c-egg rather than an increase in relative c-egg size. While this is not inconsistent with the hypothesis of Houston et al. (1983) it provides little support. Pierotti and Bellrose (1986) found that under conditions of superabundant food, Western Gulls do not

show a reduction in the size of the c-egg. This observation is consistent with the hypothesis of Houston et al. (1983) though, in the absence of an experimental study, it cannot be determined whether the large c-egg was a direct outcome of improved female condition or whether c-egg size was increased because the superabundant food indicated to the birds that there was no need for brood reduction adaptations.

The results of this study, showing an increase in the size of the c-egg following food supplementation on the day of clutch initiation, do provide support for the hypothesis of Houston et al. (1983). It appears that energetic resources are limiting the size of the c-egg. Thus, the small size may not be adaptive.

Since females are capable of laying large c-eggs if the first egg is removed, the most likely mechanism which could result in a protein shortage to the female is a change in foraging behavior as a result of the presence of an egg in the nest. In both gulls and terns, females tend to spend relatively more time on territory prior to laying than do males (Nisbet 1973, Pierotti 1981, Fitch and Shugart 1984, Maxson and Bernstein 1984). Courtship feeding during this period appears to be an important form of nutrition for the female (Nisbet 1973). An abrupt decline in courtship feeding at approximately the time of clutch initiation has been found in the Herring Gull and the Lesser Black-backed Gull (Brown 1967, Niebuhr 1981) though this does not appear to be the case in the Common Tern (Nisbet 1973). The reason for this reduction in courtship feeding is not clear. Fitch and Shugart (1984) found that both male and female attendance on territory increased during the fertile period (4 days prior to the laying of the a-egg up to the laying of the b-egg) and males spent more time with females during this period. These changes in attendance patterns could result in a decline in time available to both sexes for foraging, a decline in courtship feeding, and ultimately a decline in the size of the c-egg. The change in attendance patterns may be an adaptive mechanism by which the c-egg is made smaller; however, this would be an extremely circuitous mechanism since the female could just regulate food intake. The Black Tern, which does not show a reduction in c-egg size, exhibits relatively little nest guarding behavior between the initiation and completion of the clutch (Baggerman et al. 1956), and thus the female may be able to maintain a high protein intake. Similarly, the superabundant food available to the Western Gulls studied by Pierotti and Bellrose (1986) may provide the female with sufficient food despite changes in attendance patterns.

TABLE 11  
RELATIVE EGG SIZE WITHIN CLUTCHES IN THE LARIDAE<sup>a</sup>

Egg volume index <sup>b</sup>	Second egg as % of first	Third egg as % of first	Number of clutches	Volume/weight	Reference
Three-egg clutches:					
Ring Billed Gull ( <i>L. delawarensis</i> )					
106.0	99.3 <sup>n</sup>	96.7*	55	V	Ryder 1975 <sup>e</sup>
103.4	100.2 <sup>i</sup>	93.3 <sup>i</sup>	43	V	Vermeer 1969
Common Gull ( <i>L. canus</i> )					
97.4	100.0 <sup>n</sup>	93.6*	138	V	Varth 1968
Herring Gull ( <i>Larus argentatus</i> )					
152.7	97.4*	88.4*	453	V	Davis 1975
178.9	99.3 <sup>n</sup>	90.3*	57	V <sup>c</sup>	Paludan 1951
159.3	99.1 <sup>n</sup>	89.6*	50	V	Parsons 1975 <sup>b</sup>
154.6	100.4 <sup>n</sup>	88.9*	100	V <sup>c</sup>	Harris 1964
184.3	100.1 <sup>n</sup>	92.7*	59	V	Barth 1968
174.0	100.5 <sup>n</sup>	92.4*	76	V	Barth 1968
181.1	100.1 <sup>n</sup>	94.8*	18	V	Barth 1968
Lesser Black-backed Gull ( <i>L. fuscus</i> )					
139.7	99.5 <sup>n</sup>	90.6*	62	V <sup>c</sup>	Paludan 1951
143.5	100.0 <sup>n</sup>	94.3*	59	V <sup>c</sup>	Harris 1964
130.5	95.5 <sup>n</sup>	88.2*	8	V	Barth 1968
136.3	97.1 <sup>n</sup>	88.8*	44	V	Barth 1968
146.0	99.1 <sup>n</sup>	92.7*	68	V	Barth 1968
California Gull ( <i>L. californicus</i> )					
142.3	100.6 <sup>n</sup>	96.5*	18	W	Behle and Goates 1957
137.6	98.4 <sup>i</sup>	89.4 <sup>i</sup>	55	V	Vermeer 1969
Western Gull ( <i>L. occidentalis</i> )					
165.6	97.7 <sup>n</sup>	90.7*	32	V	Coulter, this volume
182.0	100.0 <sup>n</sup>	98.1 <sup>n</sup>	103	W	Pierotti and Bellrose 1986
Kelp Gull ( <i>L. dominicanus</i> )					
152.9	94.7 <sup>i</sup>	86.6 <sup>i</sup>	139	W <sup>d</sup>	Fordham 1964
167.3	97.1 <sup>n</sup>	90.3*	8	W	Williams et al. 1984
166.2	98.4 <sup>n</sup>	90.6*	18	V	Unpublished data <sup>f</sup>
Great Black-backed Gull ( <i>L. marinus</i> )					
198.7	101.4 <sup>n</sup>	98.0 <sup>i</sup>	35	V <sup>c</sup>	Harris 1964
222.5	102.6*	97.1*	74	V	Barth 1968
211.7	99.9 <sup>n</sup>	95.1*	93	V	Barth 1968
214.4	98.4 <sup>n</sup>	95.2*	16	V	Barth 1968
Glaucous-winged Gull ( <i>L. glaucescens</i> )					
174.2	98.8 <sup>n</sup>	92.1*	152	V	This study
Laughing Gull ( <i>L. atricilla</i> )					
75.7	97.7*	87.6*	137	W	Schreiber et al. 1979
82.7	97.1 <sup>n</sup>	91.9*	15	V	Preston and Preston 1953
Silver Gull ( <i>L. novaehollandiae</i> )					
70.6	95.8 <sup>n</sup>	89.7*	12	V	Mills 1979
75.7	101.8 <sup>n</sup>	92.8*	71	V	Wooler and Dunlop 1981 <sup>e</sup>
Black-headed Gull ( <i>L. ridibundus</i> )					
68.1	99.3 <sup>n</sup>	94.3*	105	V <sup>c</sup>	Ytreberg 1956
70.5	99.9 <sup>n</sup>	97.7*	156	V	Lundberg and Vaisanen 1979
Black-legged Kittiwake ( <i>Rissa tridactyla</i> )					
88.7	97.3*	92.7*	33	V	Coulson 1963
92.0	99.4 <sup>n</sup>	92.7*	26	W	Runde and Barrett 1981
Black Tern ( <i>Chlidonias niger</i> )					
21.4	107.4 <sup>n</sup>	102.7 <sup>n</sup>	6	V	Dunn 1979

TABLE 11  
CONTINUED

Egg volume index <sup>a</sup>	Second egg as % of first	Third egg as % of first	Number of clutches	Volume/weight	Reference
<b>Common Tern (<i>S. hirundo</i>)</b>					
38.4	96.3 <sup>i</sup>	91.6*	112	V <sup>c</sup>	Gochfeld 1977
39.4	99.6 <sup>n</sup>	97.9 <sup>n</sup>	22	V	Gemperle and Preston 1955
n.d.	97.1 <sup>i</sup>	94.6 <sup>i</sup>	33	W <sup>d</sup>	Nisbet and Cohen 1975
n.d.	99.1 <sup>i</sup>	96.7 <sup>i</sup>	64	W <sup>d</sup>	Nisbet and Cohen 1975
Average (three egg):					
	99.1 ± 2.2	92.9 ± 3.5			
<b>Two-egg clutches:</b>					
<b>Herring Gull (<i>L. argentatus</i>)</b>					
154.3	94.3*		30	V	Parsons 1975b
<b>Kelp Gull (<i>L. dominicanus</i>)</b>					
161.4	98.0 <sup>n</sup>		11	W	Williams et al. 1984
168.8	98.8 <sup>n</sup>		14	V	Unpublished data <sup>f</sup>
<b>Glaucous-winged Gull (<i>L. glaucescens</i>)</b>					
174.7	96.6*		82	V	This study
<b>Laughing Gull (<i>L. atricilla</i>)</b>					
75.1	94.3*		71	W	Schrieber et al. 1979
<b>Silver Gull (<i>L. novaehollandiae</i>)</b>					
75.8	97.8 <sup>n</sup>		51	V	Mills 1979
74.0	92.9*		238	V	Wooller and Dunlop 1981
<b>Black-legged Kittiwake (<i>Rissa tridactyla</i>)</b>					
87.8	95.9*		104	V	Coulson 1963
91.1	95.4 <sup>i</sup>		77	V <sup>d</sup>	Maunder and Trelfall 1972
88.7	95.8*		67	W	Runde and Barrett 1981
93.2	96.2*		366	W	Runde and Barrett 1981
<b>Roseate Tern (<i>S. dougallii</i>)</b>					
n.d.	95.6 <sup>i</sup>		63	W <sup>d</sup>	Nisbet and Cohen 1975
<b>White-fronted Tern (<i>S. striata</i>)</b>					
50.7	94.8*		34	V	Mills and Shaw 1980
Average (two egg):					
	95.9 ± 1.7				

<sup>a</sup> Significance as listed in source or calculated if possible (two-tailed t-test). If only length and breadth available, volume was calculated from mean values and listed as significant if both length and breadth were significant, not significant if neither was significant and not testable if one was significant. Data for more than one year are averaged (weighted) and listed as significant if any single year was significant. Data for different localities are listed separately.

<sup>b</sup> Volume (cc) is calculated as length × breadth;<sup>2</sup> volume is not corrected for shape and thus is an index only. Volumes are weighted averages of years for each egg, unweighted average of eggs.

<sup>c</sup> Variance for length and breadth only.

<sup>d</sup> No variance.

<sup>e</sup> Pairs with adult plumage only.

<sup>f</sup> Punta Tombo, Argentina, November 1983.

<sup>g</sup> Order of laying not certain.

\*  $P < .05$ , different from a-egg.

<sup>n</sup>  $P > .05$ .

<sup>i</sup> Not testable.

n.d. No data.

The presence of a small b-egg in clutches of 2 eggs (see Table 11) does not refute this hypothesis as an explanation for the reduced c-egg size. A small b-egg could result from an earlier change in attendance patterns or from a shortage of energetic reserves in the female (Houston et al. 1983). Furthermore, the reduction in b-egg size, relative to the a-egg, is less in clutches of 2 (4.1%,

$n = 13$  studies, 8 species, Table 11) than the reduction in c-egg size, relative to the a-egg, in clutches of three (7.1%,  $n = 40$  studies, 15 species, Table 11).

This interpretation of the role of energy intake during laying provides one of the strongest mechanisms that could limit clutch size to 3 eggs. Females may not have a sufficiently high rate of

protein intake following the initiation of the clutch to allow the laying of a fourth egg. Changes in attendance patterns that could increase the protein intake of the female may carry a cost for both adults in terms of an increased probability of egg predation, or a cost to the male resulting from a decreased probability of paternity.

#### THE BROOD REDUCTION HYPOTHESIS

The results of this study indicate that the presence of brood reduction adaptations are compatible with the observation that clutch size is not limited by brood-rearing capacity. There was considerable variation in the extent to which the third chick was at a competitive disadvantage. Though in no case did all chicks hatch synchronously ( $n = 54$ ), the difference in the time of hatching of the first and third chick was as little as 12 h (range 12–72 h). Pairs with relatively synchronous broods may have been those pairs capable of rearing enlarged broods. If the small c-egg is interpreted as a brood reduction adaptation (as the above analysis implies it should not be), the considerable variation in its relative size also is compatible with the view that some pairs were capable of raising enlarged broods. The volume of the c-egg was greater than or equal to the volume of the a-egg in 9.5% of clutches ( $n = 158$ , 1983–1985 combined). There was no correlation, however, between the relative size of eggs in a clutch and the degree of hatching synchrony, as could be expected if both traits are components of a brood reduction strategy.

Of greater importance, the results of this study indicate that asynchronous hatching may be beneficial regardless of the number of chicks raised. Among broods that fledged 2 chicks, the observed growth rates and timing of third chick mortality fit the predictions of the brood reduction hypothesis. There appeared to be no "cost" associated with asynchronous hatching, however, even among broods from which all chicks fledged. In contrast, synchronously hatched broods, from which all chicks fledged, had slower growth rates than control broods. The reduced growth rate in this situation could be considered further evidence in support of the brood reduction hypothesis (that is, only 2 chicks should have fledged in the slow growing synchronous broods but synchronous hatching prevented the early death of 1 chick) or else evidence suggesting that synchronous hatching would be a detriment even under conditions of abundant food.

In one other experimental study of asynchronous hatching in gulls a similar, somewhat paradoxical result was found. Hahn (1981) found that synchronous broods were less successful than control broods but not because of the predicted rapid mortality of third chicks in control broods;

instead, in most control broods all chicks survived, while in most synchronous broods 1 chick died. Hahn (1981) also concludes that asynchronous broods may be more successful regardless of food supply.

#### SUMMARY

The truncation of the clutch-size frequency distribution of many members of the family Laridae traditionally has been considered to be a result of limits imposed by the incubation capacity of the adults. The incubation capacity of the Glaucous-winged Gull results in an abrupt decline in the marginal benefit of egg production after the third egg. Because of the asymmetrical benefit of a fourth egg relative to a third it is not surprising that the distribution of clutch sizes is skewed to the left. The incubation capacity hypothesis, however, cannot explain the virtual absence of 4-egg clutches since some pairs are capable of hatching up to 5 eggs. Moreover, incubation capacity represents only a proximate limit to clutch size since there is no *a priori* reason why brood patch number or size could not be increased to increase the hatching success of large clutches.

A more important limit to clutch size in gulls may involve energetic limitations following the initiation of the clutch. Females may not have a sufficiently high rate of protein intake following the initiation of the clutch to allow the laying of a fourth egg. This factor, particularly in conjunction with the decreased marginal benefit of egg production imposed by the incubation capacity, could explain the sharp truncation at 3 eggs and could be one of the selective factors leading to a modal clutch of 3.

I found no experimental evidence that clutch size is limited by energetic resources during the pre-laying period. The evidence from non-experimental studies, however, suggests that pre-laying energetics does influence egg production. The reason for this difference is not clear, but it would appear that energetic costs of egg production during the pre-laying period cannot be ruled out as another potential cost associated with the production of a fourth egg.

While this study found that the presence of brood reduction adaptations was compatible with the assumption that clutch size is not limited during the chick-rearing period, it also cast doubt on the general applicability of the brood reduction hypothesis to gulls and terns. The small c-egg, generally assumed to be an adaptation for brood reduction, may instead be a non-adaptive consequence of energy shortages during laying. Moreover, this study indicates that asynchrony may be advantageous regardless of the number of chicks that can be raised. Thus, asynchrony is

apparently an adaptation for maximal growth under any circumstance rather than an adaptation for food stress.

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