SHORT COMMUNICATIONS

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Fledging success of experimentally enlarged broods of the Glaucous-winged Gull.—Lack's (1947, 1948) hypothesis that the most common clutch size in a population reflects the maximum number of young that can be adequately fed by the parents has stimulated much research. Several experimental studies have supported his hypothesis (see Klomp 1970, Crossner 1977, Högstedt 1980); however, numerous exceptions exist in which the most productive brood size is larger than the most common brood size (e.g., see Klomp 1970, Haartman 1971, Bryant 1975, Schifferli 1978). Stimulated in part by these exceptions, Charnov and Krebs (1974) modified Lack's hypothesis to incorporate the "cost of reproduction" (see also Bryant 1979, Ricklefs, 1983, Nur 1984). Charnov and Krebs (1974) argued that the most common clutch size may be smaller than the most productive clutch size if the survival or future fecundity of adults rearing larger clutches is reduced. Several species in the genus *Larus* are capable of rearing broods larger than the most common clutch size. Gulls generally lay 2–3 eggs; however, in at least four species, adults are capable of rearing more than three young (Herring Gull [*Larus argentatus,* Haymes and Morris 1977]; Glaucous-winged Gull [*L. glaucescens,* Vermeer 1963, Ward 1973]; Lesser Black-backed Gull [*L. fuscus,* Harris and Plumb 1965], Western Gull [*L. occidentalis,* Coulter 1973]). However, in none of these studies has both the breeding success and survival of adults rearing enlarged broods been monitored. Thus it is not possible to distinguish between two hypotheses accounting for the ability of gulls to raise extra chicks: (1) because of a surplus of food the potential productivity of gulls is now greater than it was during the period when the three-egg clutch evolved (Lack 1966); or, (2) although gulls can raise more than three chicks, the cost to the adult resulting from decreased adult survival exceeds the benefit of more young fledged (Ward 1973). To address these hypotheses, I examined factors influencing clutch size in the Glaucous-winged Gull, and I report here on the ability of Glaucous-winged Gulls to raise enlarged broods. I assess chick growth rate, condition, and fledging success in broods of different size. I also examine the relationship between parental investment and chick growth.

Methods.—Glaucous-winged Gulls were studied on Protection Island, Washington (48°07'N, 122°55'W) between May and August of 1983–1985. Each year I manipulated the brood size of approximately 200 nests to create broods of 1–7 chicks (normal range 1–3). Chicks less than two days old were added to, or removed from, nests within two days of the hatching of the eggs in the nest. In each year, I established broods of 1, 2, 3, 5, and 7 chicks at approximately 31 nests (range 18–55) each. In 1984, I also established broods of 4 and 6 chicks.

I monitored fledging success at 172 nests in 1983, 176 nests in 1984, and 156 nests in 1985. I considered a chick to be fledged if it survived to at least day 30. Chicks alive at day 30 and subsequently found dead were counted as not-fledged. Glaucous-winged Gulls do not actually fledge until day 37–57 (Vermeer 1963); however, most chick mortality occurs in the first four weeks of life (Vermeer 1963, Reid 1987). Although fledging age increased with brood size (see below), this did not bias the determination of fledging success. Chicks from all brood sizes that survived to day 30 were large (>800 g) and were readily found if they died prior to fledging. Statistical analyses of fledging success were performed on log-transformed data (log[number fledged + 1]) to meet the assumption of homoscedasticity of variance.

I weighed and measured chicks at 136 nests in 1983, 176 nests in 1984, and 200 nests in 1985. All weights and measurements were log-transformed prior to analysis. I examined the size of chicks at two ages: during the intervals of 18–24 days (9–15 in 1983) and 31–

TABLE 1

PRINCIPAL COMPONENT LOADINGS OF BODY SIZE MEASUREMENTS AT THREE CHICK AGES AT EXPERIMENTALLY SYNCHRONIZED NESTS IN 1985. THE MAGNITUDE OF THE LOADING REFLECTS THE CORRELATION BETWEEN A GIVEN VARIABLE AND THE FIRST PRINCIPAL COMPONENT

	Chick age		
	Day 1	Day 20	Day 31
Culmen	0.358	0.767	0.644
Tarsus	0.847	0.865	0.800
Wing	—	0.732	0.473
Weight	0.921	0.813	0.837

41. I adjusted the weights and wing lengths of chicks to the mid-point of these intervals using the slopes of regressions of weight and wing length on age. The growth analysis was performed on the mean adjusted chick weight and wing length for each nest. Neither weight nor wing length differed from a normal distribution in either chick age-group in any year (Kolmogorov-Smirnov Test, all groups: $P > 0.05$). I performed the analysis on two subsets of the data, first using all chicks measured during these two periods (N = 783 chicks) and second, excluding chicks that were known to die prior to fledging (resulting sample N = 593 chicks). The first method of analysis reflects the growth of the entire brood; the second method is a better indication of the condition of chicks that actually fledge.

I examined the influence of time allocation by the adults on the growth rate of chicks among experimentally synchronized broods of two chicks established in 1985. To control for effects of brood size and hatching date, I manipulated the brood size and phenology of 52 nests visible from three elevated blinds. I replaced the chicks present at each nest with two newly hatched chicks over a three-day period (July 7–9). All of the nests visible from a given blind were given the two chicks on the same day so that by watching nests from the three blinds on three successive days, I observed adults feeding chicks of identical age that had hatched over a three-day interval. Some chicks died during the course of the season; to avoid the confounding effect of differences in brood size, I analyzed only nests that had two chicks on the day of observation.

Observations of the nests were made at chick ages 17, 28, and 43. Each period of observation was 10 h and began between 06:00 and 06:20 (total observation time 90 h; 1560 nest-h). The nests were scanned every 10 min and the presence or absence of each adult was recorded. I analyzed the percent of total observation time that each adult was absent from the territory, averaged for the members of the pair. Arcsine square-root transformed values of the percent time absent from the territory did not deviate significantly from a normal distribution and were analyzed by Pearson correlation.

On days, 1, 20, and 31, the chicks at the experimentally synchronized nests were weighed, and the culmen, tarsus, and wing chord (only on day 20 and 31) were measured. The measurements on days 20 and 31 were made three days after the pattern of time allocation at these nests was measured. All chick measurements were log-transformed. Using only nests that had two chicks on the day of measurement, I used principal components analysis to create a "body size" factor for the chicks at each age (Table 1). Chick size on day 20 and day 31 was significantly correlated with size on day 1 (day 20: $r = 0.36$, $P < 0.001$, N = 74; day 31: $r = 0.33$, $P < 0.01$, N = 68). I removed the effect of initial size by regressing

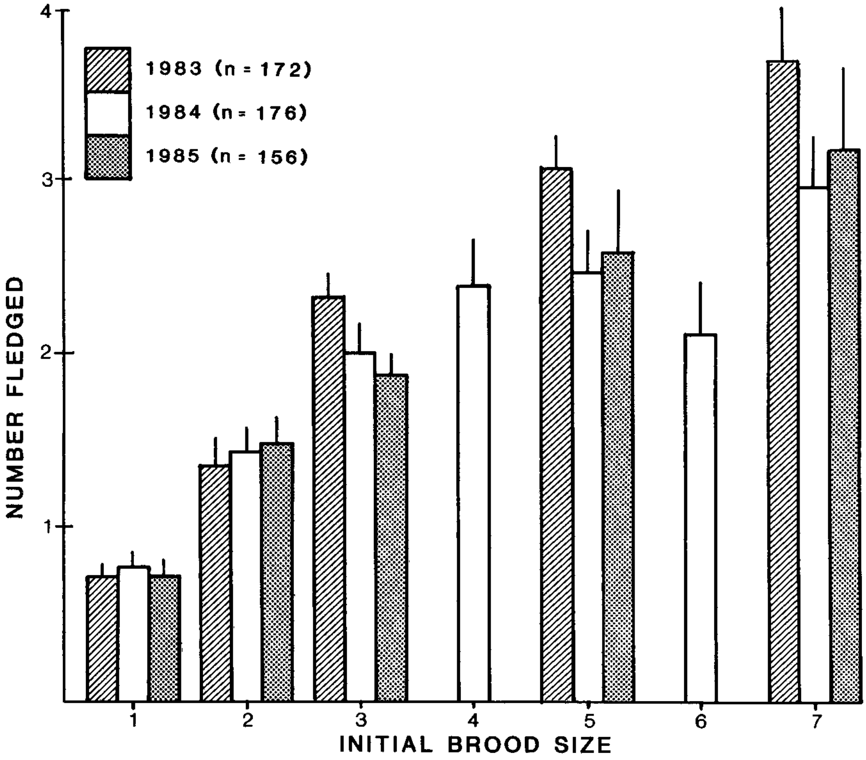

FIG. 1. Fledging success as a function of brood size in 1983–1985. The top of each bar is the mean, and the vertical line represents one SE.

the size on day 20 and 31 against the size on day 1 and calculating the residual size of each chick. The residual sizes of the two chicks at each nest were then averaged for each nest, and this value was used in the subsequent analysis.

To measure the effect of brood size on the length of the nestling period, I scored the stage of plumage development of chicks older than 25 days at 63 nests in 1984. The last portion of the body to molt to juvenal plumage is the neck and head. I scored the percent of the head that had molted to juvenal plumage to the nearest 25%. This measure provides an index of the stage of development as the chicks approached fledging; no chicks were observed flying with more than 25% natal plumage on the neck and head. I calculated the mean molt score for chicks at each nest for each day of observation.

Results.—In each year, the fledging success among nests with artificially enlarged broods exceeded the success of nests with normal brood sizes (Fig. 1; correlation of number fledged with brood size, 1983: $r_s = 0.74$, $P = 0.001$, N = 172 nests; 1984: $r_s = 0.52$, $P = 0.001$, N = 176; 1985: $r_s = 0.46$, $P = 0.001$, N = 156). Highest fledging success was found in broods of seven chicks ($\bar{x} = 3.29 \pm 1.76$ SD, N = 79 nests). Fledging success of the most common brood size, three chicks, was 2.05 ± 0.92 chicks (N = 109).

TABLE 2

The Effect of Brood Size and Hatching Date on Chick Growth. Stepwise Linear Regression with Brood Size Entered on Step 1. Sample Size Refers to the Number of Nests (Measurements for Chicks at Each Nest Were Averaged). The Regression Coefficient Is the Standardized Coefficient in the Complete Model

	Regression coefficients							
	Young chicks				Old chicks			
Year	Brood size	Hatch date	R^2	N	Brood size	Hatch date	R^2	N
Weight								
1983	−0.194	−0.076	0.050	80	−0.340[b]	−0.083	0.127[a]	63
1984	−0.464[c]	−0.075	0.223[c]	141	−0.535[c]	−0.078	0.313[c]	73
1985	−0.261[a]	0.050	0.065	85	−0.281[a]	−0.007	0.080	69
Wing length								
1983	−0.169	−0.085	0.042	80	−0.185	0.011	0.034	63
1984	−0.462[c]	−0.183[a]	0.254[c]	141	−0.549[c]	−0.252[b]	0.433[c]	73
1985	−0.275[b]	−0.165	0.122[b]	85	−0.366[c]	−0.160	0.183[c]	69

[a] $P < 0.05$.

[b] $P < 0.01$.

[c] $P < 0.001$.

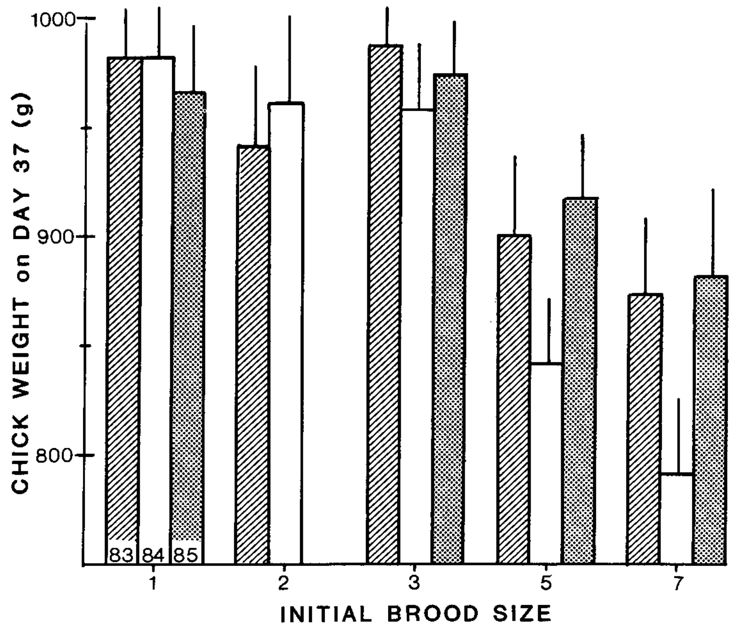

Fig. 2. Chick weight on day 37 as a function of brood size. Original analysis on log-transformed data. Sample size: 1983, N = 63; 1984, N = 73; 1985, N = 69.

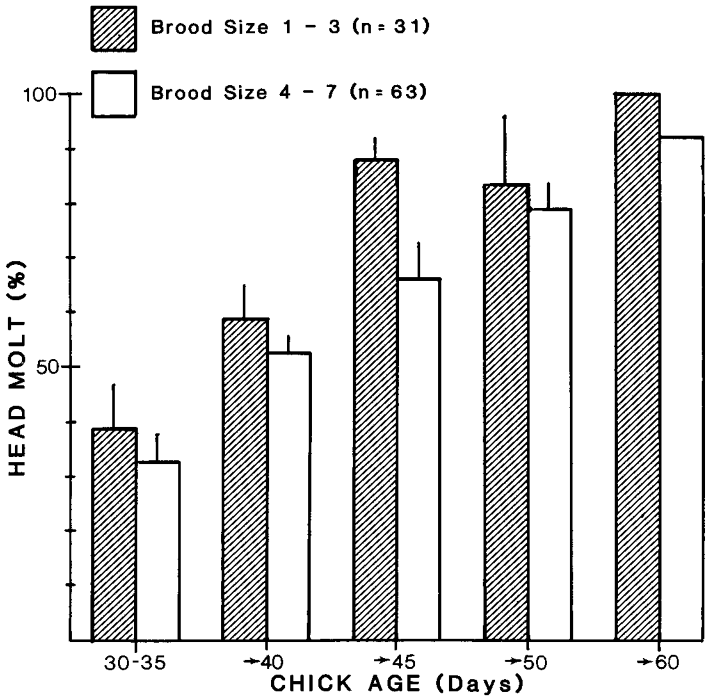

FIG. 3. Chick development as a function of brood size. Stage of development scored as the percent of head and neck molted to juvenal plumage.

Average weight and wing length decreased significantly with brood size in all years and at both chick ages (Table 2, Fig. 2). Among older chicks in 1984, brood size alone explained 31% of the variation in the weight of chicks and 37% of the variation in wing length. In 1983 and 1985, brood size accounted for less then 16% of the variation in any measurement. The analysis of growth rate as a function of brood size (Table 2, Fig. 2) includes chicks that were known to die prior to fledging. I repeated the analysis, excluding chicks that did not fledge to obtain a more accurate measurement of the influence of brood size on the condition of chicks that fledge. The resulting pattern of correlations differed only slightly from the entire sample.

I examined the growth of broods of potentially high-quality adults by restricting the sample to only those pairs that fledged within one chick of the initial brood size. Among these pairs, the correlations between chick growth and brood size are reduced. In this restricted sample, initial brood size accounts for a maximum of only 17% ($\bar{x}$ = 8.0%) of variation in size and the relationship is significant among old chicks in 1984 (weight: $r = -0.35$, $P < 0.05$, N = 40; wing: $r = -0.39$, $P < 0.01$, N = 40). Nevertheless, all correlations (at both chick ages) were negative; thus, even among those adults that were capable of rearing large broods, the chicks fledged in poorer condition.

At experimentally synchronized nests in 1985, chick size increased significantly with the percent of time each adult was off territory at both day 20 ($r = 0.33$, $P = 0.024$, N = 37) and day 31 ($r = 0.33$, $P = 0.026$, N = 35).

The stage of plumage development (percent head molt) was negatively correlated with brood size after adjusting for chick age (Fig. 3; $B = -0.244$, partial $r = -0.201$, $P = 0.001$, $N = 94$; effect of chick age removed in step 1 of stepwise regression, slope of regression of percent head molt with chick age: $B = 0.697$, partial $r = 0.70$, $P < 0.001$). By day 40 the development of chicks in enlarged broods was roughly five days behind the development of chicks in normal broods (Fig. 3).

Discussion.—Four species of gulls are capable of increasing parental effort sufficiently to allow more than three chicks to be fledged (Vermeer 1963, Harris and Plumb 1965, Ward 1973, Coulter 1973, Haymes and Morris 1977). It is unlikely that the ability to raise more than three chicks is solely a result of the presence of artificial food sources (cf., Lack 1966, Haymes and Morris 1977), given the consistency of the pattern among species and habitats. Moreover, Ward (1973) found that experimentally enlarged broods of Glaucous-winged Gulls could be reared at colonies at which the birds did not have access to artificial food sources.

In this study, fledging success increased with brood size up to broods of seven chicks. However, chick weight and wing length decreased and the nestling period increased with brood size. The most pronounced decline in chick condition occurred among broods of 4–7 chicks; there was relatively little variation in chick condition among broods of 1–3 chicks (Fig. 2). Even among small broods (two chicks), chick growth rate varied as a function of time spent foraging by the adults. Thus, the growth rate of chicks at all brood sizes seems to represent the optimal growth rate from the perspective of the parents rather than the maximal growth rate of the chick.

Because of the decline in chick condition among chicks in enlarged broods, postfledging survival, rather than fledging success, most directly addresses Lack's (1947, 1948) hypothesis. Based on postfledging survival, the most productive clutch size of the Glaucous-winged Gull has been found to differ between locations and years. Vermeer (1963) found that postfledging survival of chicks in artificially enlarged broods was higher than that of chicks in control broods, based on off-colony sightings. However, Ward (1973) reanalyzed Vermeer's data including later sightings and found that the number of chicks surviving after fledging was maximal in broods of three, although broods of five were only slightly less productive. In three other experimental manipulations of the brood size of the Glaucous-winged Gull, Ward (1973) found that in two years (in two different colonies) broods of six chicks had the highest number of chicks surviving after fledging and, in one year, broods of three had the highest success. Fledging weights of chicks in artificially enlarged broods show equally inconsistent results. Haymes and Morris (1977) found no difference in the fledging weights of chicks in control broods and artificially enlarged broods (up to five chicks) of Herring Gulls. In the Glaucous-winged Gull, Ward (1973) found no difference in fledging weights in broods of 1–6 chicks at one study site but found a decline in fledging weight with brood size at another site. Coulter (1973) found a decline in weight with brood size (up to six chicks) in the Western Gull.

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Fall migration of Ruby-throated Hummingbirds in the northeastern United States.—The Ruby-throated Hummingbird (*Archilochus colubris*) migrates long distances between its breeding range in eastern North America and its winter range in the southern United States and Middle America (Bertin 1982, A.O.U. 1983). Most references to the overland migration of Ruby-throated Hummingbirds concern their regional status or report large numbers of fall migrants, while behavioral, ecological, and energetic aspects of their migration have received little attention. The ridges of the Appalachian Mountains are major routes for southbound migrants, and in this study we describe the seasonal and daily timing of migrating Ruby-throated Hummingbirds and the influence of wind direction and velocity at one such Appalachian lookout, Hawk Mountain Sanctuary, Pennsylvania. We also present data from