

# BENIGN NEGLECT OF TERMINAL EGGS IN HERRING GULLS<sup>1</sup>

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**Abstract.** Terminal-egg neglect arises in Herring Gulls (*Larus argentatus*) when parents begin to feed and brood the first two (a-, b-) newly hatched young, thereby disrupting incubation of the third (c-) egg. Mean temperature of pipped c-eggs dropped to 33.4°C, significantly below that of the pipped a- (37.6°C) and b- (36.6°C) eggs. Experimental manipulation of neglect by placement of pipped c-eggs at chronologically earlier nests showed that both hatchability and time to hatch were unaffected by natural levels of neglect. Laboratory incubation confirmed that chilling pipped eggs to 33°C does not affect hatching. Further chilling to 30°C lowered hatchability and increased hatching times. Development was arrested at 27°C. Although Herring Gulls clearly neglected terminal eggs during the final stages of incubation, it was entirely benign in that mean embryonic temperatures were maintained above levels that would cause damage. Last-hatched eggs in this species are evidently well-adapted, physiologically, to withstand chilling down to at least 33°C, thereby enabling them to maintain full viability despite moderate levels of neglect during the hatching period.

**Key words:** Egg neglect; incubation temperature; parental care; Herring Gulls.

## INTRODUCTION

Terminal-egg neglect arises during the hatching period in some birds when parents begin caring for first-hatched young, thereby reducing attentiveness towards unhatched eggs remaining in the nest. Neglect of terminal eggs is found mainly in species with asynchronously hatching young and open, ground-level nests conducive to movements of parents and newly hatched young (Evans and Lee 1991, see also Beissinger and Waltman 1991).

Neglect can selectively increase the incubation period of terminal eggs (Nice 1954, Greenlaw and Miller 1983). Hatching delay of terminal eggs can have negative effects if it increases hatching asynchrony and thereby reduces competitive ability of the last-hatched young (Forbes and Ankney 1988, Slagsvold 1985, Amundsen and Stokland 1988). Retarded development resulting from low incubation temperatures is well documented (Lundy 1969, Webb 1987). There are also several accounts of terminal-egg mortality attributed to neglect or desertion during the final stages of incubation (Beer 1962, 1966; Drent 1970; Reid 1987; Beissinger and Waltman 1991; reviewed in Evans and Lee 1991).

Although terminal-egg neglect and its possible consequences have been reported for several spe-

cies, apart from work with the altricial American White Pelican (*Pelecanus erythrorhynchos*) (Evans 1990a, 1990b), little is known of incubation temperatures during the pipped egg stage, and there apparently have been no other attempts to test experimentally the presumed negative effects of natural levels of neglect on hatchability or hatching times (but see Reid 1987). Here we describe terminal-egg neglect in Herring Gulls (*Larus argentatus*) and test the effects of such neglect on survival, hatching times, and neonatal growth rates using a combination of field and laboratory experiments.

Herring Gulls are monogamous and colonial (Burger 1984). Both sexes incubate and care for the young at flat, open nests placed on the ground or, less commonly, on rocks or small cliffs. The normal clutch size is three (designated a-, b-, and c- on the basis of laying order) which hatch over a period of from two to three days (Drent 1970, Parsons 1972, Hebert and Barclay 1986). Asynchronous hatching establishes a significant within-brood size hierarchy, which commonly results in differential mortality of the terminal, or c-offspring (Graves et al. 1984, Hebert and Barclay 1986).

Herring Gulls begin to feed their semi-precocial young on the day of hatching, first at the nest site, then on adjacent portions of their territory (Tinbergen 1953, Haycock and Threlfall 1975, Graves et al. 1984). These movements, combined with asynchronous hatching within the

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brood, can lead to a significant disruption of incubation during the time that the last-laid egg is breaking through the shell in preparation for hatching (pipped egg stage) (Paludan 1951, Drent 1970). Neglect during the pipped egg stage has been interpreted as a cause of mortality in a significant proportion (up to 11%) of Herring Gull terminal eggs on a study site in Newfoundland (Haycock and Threlfall 1975) and has been recognized as a source of mortality in other populations (Drent 1970).

## METHODS

Incubation behavior and egg temperatures were examined at a Herring Gull colony located on Kent Island, New Brunswick, Canada. The study area was censused once daily during egg laying from 20 May to 17 June 1986 and from 18 May to 19 June 1987. Each new nest with eggs was marked individually with a numbered wooden stake. Eggs were individually marked according to their laying order with a permanent felt-tip marker. Observation blinds were set up in the colony prior to the completion of laying.

## INCUBATION AND RELATED BEHAVIOR

To document changes during the transition from incubation to care of chicks, behavior at focal nests was observed from within a blind throughout the incubation and hatching periods (mid-May to late July) in 1986. One nest was observed during each 1-hr sampling period. Behaviors recorded were time spent off the nest, duration of sitting spells, occurrence of rising and resettling, whether settlements were 'complete' (if they contained quivering, Beer 1961), number of times egg positions were changed (egg shifts), and feedings on the nest. Fifty-four nests were observed over the first 25–26 days of incubation beginning with the laying of the c-egg and ending before the onset of pipping. These nests were observed an average of 2.3 times each over this period for a total of 124 hr of observation. In addition, 24 nests where the a-egg was pipped (a-pip stage), 13 nests where the a-egg was hatched and the b-egg was pipped (b-pip stage), and 14 nests where the a- and b-eggs were hatched and the c-egg was pipped (c-pip stage) were also observed for 1 hr each.

In 1987, observations began at the onset of pipping. In addition to the above mentioned behaviors, all feedings off the nest were noted. Behavior was recorded in 1987 at 12 a-pip nests,

15 b-pip nests, and 20 c-pip nests. Samples taken at a- and b-pip nests were for 1 hr, as before. To obtain more information on chick feeding and other potential proximate causes of parental incubation responses during the c-pip stage, samples taken at this time were extended to 2 hr and were taken when the b-chick was approximately one day old. When measures were compared between stages, hourly rates were used. In this and subsequent sections, non-parametric statistical tests (Daniel 1978) were employed when data were non-normal or had unequal variances. Other tests followed Zar (1974) and the SAS Institute (1985). Where results for the two years were not significantly different, they were combined for further analyses. Paired comparisons following significant analyses of variance (ANOVA) were limited to tests of *a priori* predictions of increasing neglect as hatching proceeded ( $a < b < c$ ). Data from the pre-pip stage of incubation are included for illustrative purposes.

## EGG TEMPERATURES

Pipped egg temperatures were determined to the nearest 0.1°C with a Yellow Springs Instruments Thermistemp model 46TUC temperature meter. The tip of a 2.8 mm flexible thermistor (YSI probe #402) was inserted about 2 cm directly down into the pip hole so that it was surrounded by body parts of the embryo. The probe was secured to the outside of the egg with tape and attached with an extension cable leading to the temperature meter placed in a blind. Parents appeared unaffected by the probes. Temperature readings were begun only after parents had returned to the nest. Records were then taken manually every 10 min for 1 hr at each nest. Temperatures of 43 pipped eggs, 14 or 15 at each stage (a-pip, b-pip, and c-pip) were recorded, using the same methods for each pip stage over the two years of the study.

## EFFECTS OF TERMINAL-EGG NEGLECT

Effects of neglect were examined experimentally in the field in 1987. Nests for this experiment were checked twice daily, at approximately 12-hr intervals, starting just before the expected onset of pipping. C-eggs from 36 experimental nests were removed at the first sign of pipping of the corresponding a-eggs, and each was put into a surrogate nest chosen to ensure that the experimental c-egg would have time to hatch before the other two eggs in the surrogate nest. C-eggs

were replaced at experimental nests with unpipped eggs from elsewhere in the colony to maintain the normal three-egg clutch. Because the experimental c-eggs were the first to hatch within their surrogate clutches, they would not have been subject to incubation disruption and neglect resulting from parents tending previously-hatched siblings. Upon hatching, the experimental c-chicks were returned to their home nests and the replacement eggs returned to theirs. C-eggs at 44 additional control clutches were handled, then left in their own nests where they were assumed to be subject to natural levels of neglect after hatching of their older siblings. Laying intervals between a- and c-eggs did not differ (unpaired *t*-test,  $P = 0.44$ ) between controls (4.96 days) and experimentals (5.14 days).

Chick masses were measured to the nearest 0.1 g with Pesola scales at hatching, then daily for seven days. Hatchability, hatch intervals, hatch mass, growth, and survivorship to seven days were determined and compared between controls and experimentals. Growth rate (ln g/day) for each chick was calculated using linear regression (Hebert and Barclay 1986). A nest was removed from the analysis if the c-chick died before it was four days old, or if the a- or b-chicks died before the end of the experiment. Growth rates were then compared using the SAS statistical test for homogeneity of slopes (GLM) (SAS Inst. 1985). The use of survival and mass data for only the first seven days after hatching was justified because most pre-fledging mortality in this species occurs within that time (Kadlec et al. 1969, Haycock and Threlfall 1975).

#### EFFECTS OF CHILLING IN THE LABORATORY

Effects of egg chilling during the final stages of incubation were studied in the laboratory with eggs collected in 1989 and 1990 from Herring Gull colonies in Manitoba, Canada. Herring Gull breeding distribution is continuous between Manitoba and the Bay of Fundy where the field studies were done, and the entire population is a single subspecies (Godfrey 1966). Clutches of three eggs were collected before the occurrence of any externally visible signs of pipping, and placed in a circulating air incubator at  $37.8 \pm 0.5^\circ\text{C}$  and approximately 65% relative humidity. Upon external pipping (shell cracked sufficiently to feel rough to the touch) of the a-egg within a clutch, the entire clutch was assigned either to a control or experimental temperature, in alter-

nating order. Eggs were then examined every 3–5 (usually 4) hr, to determine the time of hatching (young chick free of shell).

In 1989, 10 clutches (experimentally chilled) were incubated at  $33 \pm 0.5^\circ\text{C}$ , and 10 clutches (controls) at  $37.8 \pm 0.5^\circ\text{C}$ . Thirty-three degrees Celsius was similar to the lowest yearly mean temperature for pipped c-eggs recorded in the field. The control temperature was similar to that commonly used for domestic fowl, and was close to the mean levels obtained for Herring Gull pipped a-eggs in the field (see results). To extend the lower range of temperatures tested, the experiment was repeated in 1990, with 10 control clutches and 10 experimental clutches incubated from a-pip onwards at each of 30 and  $27^\circ\text{C}$ .

## RESULTS

### INCUBATION AND RELATED BEHAVIOR

Parents rarely left the nest uncovered prior to the onset of pipping or during the a-pip stage (Table 1). After the onset of pipping, there was no difference between years in the amount of time the parents spent off the nest (Mann-Whitney *U*-test,  $P > 0.2$ ). For both years combined, time off the nest increased significantly during successive pip stages (Kruskal-Wallis ANOVA,  $P < 0.0001$ ; Mann-Whitney *U*-test, a- vs. b-,  $P < 0.02$ , b- vs. c-,  $P < 0.001$ ).

Feedings of young away from the nest contributed substantially to the time parents spent off the nest during the c-pip stage. Twenty 2-hr observation periods in 1987 at nests where the b-chick was approximately one day old, yielded 77 feedings, with a mean of  $1.9 \pm 1.4$  feedings/hr/nest. Forty-three percent of these feedings were performed away from the nest. The parent clearly led the chick(s) off the nest in 77% of the feedings that occurred away from the nest.

Besides time spent feeding chicks, parents also spent time off the nest standing or sitting nearby during the c-pip stage (when the b-chick was one day old). Preening sometimes also occurred at this time. An average of 25% of the time ( $n = 20$  nests) that the attending parent was off the nest was spent in these activities.

Results of the other measures of incubation behavior are given in Table 2. The duration of sitting spells declined significantly as hatching progressed (Kruskal-Wallis ANOVA,  $P < 0.0001$ ). The number of times the incubating parent rose and resettled on the eggs increased

TABLE 1. Incubation neglect (min off nest/hr) of Herring Gull eggs at various stages of incubation.

Stage	Mean $\pm$ SE	Range	<i>n</i> <sup>a</sup>
Pre-pipping	2.8 $\pm$ 0.2	0–17	54
a-pip	3.3 $\pm$ 0.1	0–14	36
b-pip	11.3 $\pm$ 0.5	0–60	28
c-pip	23.6 $\pm$ 0.4	0–60	34

<sup>a</sup> Number of nests.

significantly ( $P < 0.001$ ), while the number of egg shifts declined ( $P < 0.002$ ). The percent of settling sequences that were complete, an indication of how well parents fit the eggs to their brood patches (Beer 1961), differed significantly between years (Mann-Whitney  $U$ -test,  $P < 0.001$ ). For each year the percent of complete settlings declined significantly as hatching progressed (1986,  $P < 0.0001$ ; 1987,  $P < 0.001$ ).

#### EGG TEMPERATURE

Along with incubation neglect came a drop in egg temperature (Table 3). There were no significant differences between years ( $P > 0.20$ ). For both years combined, temperatures were different during each pip stage (overall,  $P < 0.001$ ; a- vs. b-,  $P < 0.05$ ; b- vs. c-,  $P < 0.01$ ). Variance in egg temperature was not homogeneous among groups (Table 3, Levene's test  $P = 0.005$ ). Greater variance and lower range while the c-egg was pipping reflected the frequent rising and resettling on the nest and longer periods off the nest at that time, causing egg temperature to fluctuate much more widely than previously. Mean ambient temperature was always lower than egg temperature (Lee 1988), indicating that cooling of c-eggs could be directly related to reduced effectiveness of incubation.

#### EFFECTS OF TERMINAL-EGG NEGLECT

Hatchability did not differ significantly (Log-likelihood test,  $P > 0.1$ ) between neglected (con-

TABLE 3. Herring Gull pipped-egg temperatures ( $^{\circ}$ C).

Egg	Mean $\pm$ SE	Range	<i>n</i>
a-pip	37.6 $\pm$ 0.21	34.9–39.4	15
b-pip	36.6 $\pm$ 0.38	31.4–39.4	14
c-pip	33.4 $\pm$ 1.02	22.0–38.7	14

trol) (84%) and unneglected (experimental) (97%) c-eggs. One a- and two c-eggs died during pipping at control nests, and one experimental c-chick died immediately after hatching. Mortality during hatching was too rare to merit statistical inferences. Hatching weight of experimental and control c-chicks were virtually identical (controls: mean  $\pm$  SE = 60.5  $\pm$  5.8 g,  $n = 31$ ; experimentals: 60.2  $\pm$  4.7 g,  $n = 34$ ;  $P = 0.49$ , unpaired  $t$ -test).

The interval between pipping and hatching (pip-hatch interval) was similar for neglected and unneglected c-eggs (Fig. 1a, Median test,  $P > 0.25$ ). Despite this similarity in pip-hatch intervals, overall hatching asynchrony within clutches (a–c hatch interval) was significantly less in nests with neglected c-eggs than in nests where c-eggs were not subject to neglect (Fig. 1b). A significantly higher proportion of nests had a–c hatch intervals less than the sample median when c-eggs were neglected (71.9%,  $n = 32$  nests) than when c-eggs were not neglected (42.3%,  $n = 26$  nests) ( $\chi^2 = 4.023$ ,  $P < 0.05$ ).

At nests where all eggs hatched, survival to seven days of age did not differ between experimentals and controls. C-chicks survived to seven days of age at 81.5% of 27 broods where c-eggs were neglected and at 80.0% of 30 broods where c-eggs were not neglected ( $\chi^2 = 0.038$ ,  $df = 1$ ,  $P > 0.75$ ). Growth rates of chicks from neglected c-eggs were significantly higher ( $P = 0.014$ ) over the first seven days (0.093  $\pm$  0.007 ln g/day,  $n = 21$ ) than for chicks from unneglected c-eggs (0.070  $\pm$  0.006 ln g/day,  $n = 25$ ). Total weight

TABLE 2. Incubation behaviors (median  $\pm$  SE of the median) of Herring Gulls during the hatching period.

Variable	Year	Stage		
		a-pip	b-pip	c-pip
Sit spells (min)	1986–87	11.00 $\pm$ 2.51 <sup>a</sup>	5.85 $\pm$ 1.36 <sup>a</sup>	3.70 $\pm$ 0.40 <sup>b</sup>
Settlings/hr	1986–87	3.00 $\pm$ 0.58 <sup>a</sup>	5.00 $\pm$ 0.87 <sup>b</sup>	6.25 $\pm$ 0.87 <sup>b</sup>
Egg shifts/hr	1986–87	1.00 $\pm$ 0.58 <sup>a</sup>	0.00 $\pm$ 0.00 <sup>b</sup>	0.00 $\pm$ 0.00 <sup>b</sup>
Complete settlings (%)	1986	75.00 $\pm$ 10.97 <sup>a</sup>	7.00 $\pm$ 7.79 <sup>b</sup>	0.00 $\pm$ 2.89 <sup>b</sup>
	1987	53.00 $\pm$ 23.09 <sup>a</sup>	0.00 $\pm$ 9.53 <sup>b</sup>	0.00 $\pm$ 0.00 <sup>b</sup>

<sup>a,b</sup> Medians in the same row having different superscripts are significantly different (Mann-Whitney  $U$ -test,  $P < 0.05$ ). Years were significantly different for Complete settlings, hence they were not combined.

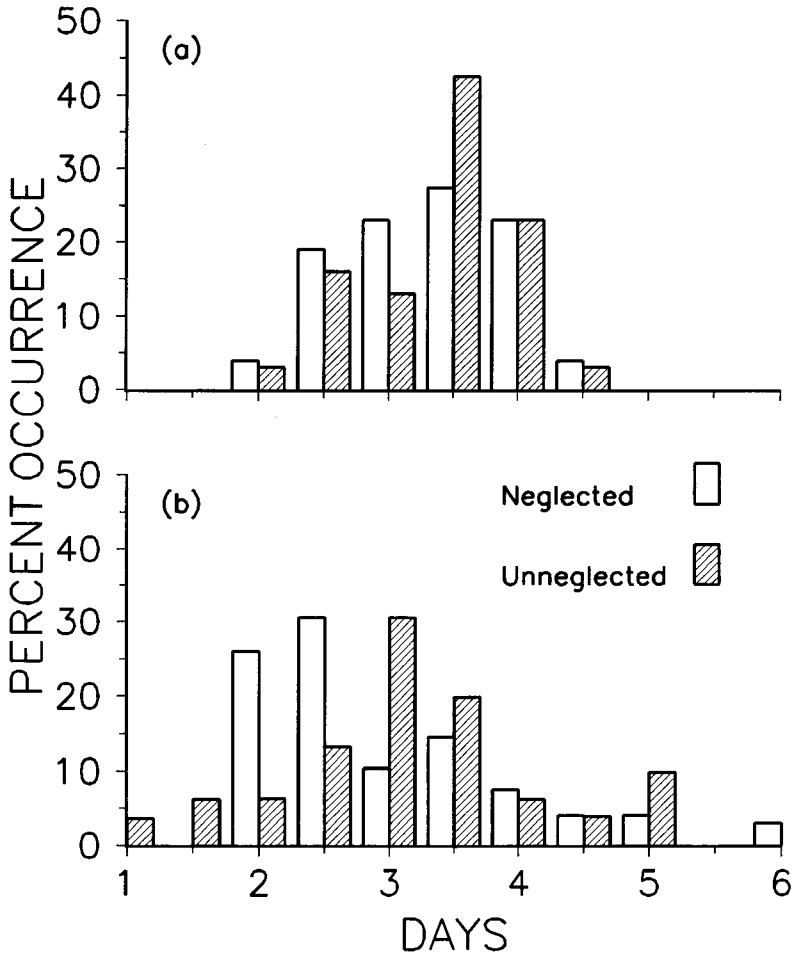


FIGURE 1. (a). Pip-hatch intervals of neglected ( $n = 30$ ) and unneglected ( $n = 35$ ) c-eggs. (b). A-c hatch intervals at nests where c-eggs were neglected ( $n = 26$ ) and unneglected ( $n = 32$ ).

gained to day seven by c-chicks also favored those from neglected c-eggs ( $37.6 \pm 17.4$  g) over those from unneglected c-eggs ( $28.3 \pm 17.8$  g), but the difference was not significant ( $P = 0.10$ , unpaired  $t$ -test).

Measures of survival, growth, pip-hatch intervals, and a-b or b-c hatch intervals were not significantly different ( $P > 0.05$ ) between experimentals and controls for a- and b- offspring (Lee 1988). Most measurements thus provided no evidence for effects of the experimental treatment. The two measures that were affected indicated that terminal-egg neglect was associated with shorter a-c hatch intervals and higher c-chick growth rates relative to nests where c-egg neglect did not occur.

#### EFFECTS OF CHILLING IN THE LABORATORY

All 27 control eggs placed in a laboratory incubator hatched in 1989. In 1990, two of 27 control eggs were either infertile or died before pipping, while a third died during the pipped egg stage. For eggs chilled to  $33^{\circ}\text{C}$ , two were added and one died at the pipped egg stage. Excluding the added eggs, the effect on hatchability was not significant ( $\chi^2 = 3.3 \times 10^{-4}$ ,  $P > 0.95$ ). At  $30^{\circ}\text{C}$ , there was a significant reduction in hatchability, with only eight of 30 (26.7%) eggs hatching (experimentals vs. controls:  $\chi^2 = 19.89$ ,  $df = 1$ ,  $P < 0.001$ ). There was an additional significant decrease in hatchability at  $27^{\circ}\text{C}$ , when none hatched (30 vs.  $27^{\circ}\text{C}$ :  $\chi^2 = 7.07$ ,  $P < 0.01$ ).

TABLE 4. Mean ( $\pm$ SE) pip-hatch intervals (hr) of Herring Gull eggs incubated at different temperatures in the laboratory.<sup>a</sup>

Year	Controls			Experimentals		
	Temperature (°C)	n eggs	Pip-hatch interval	Temperature (°C)	n eggs	Pip-hatch interval
1989	37.8	27	65.0 $\pm$ 3.7	33.0	27	71.5 $\pm$ 4.3
1990	37.8	24	67.4 $\pm$ 3.0	30.0	8 <sup>b</sup>	95.1 $\pm$ 10.0

<sup>a</sup> Chilling of all eggs within an experimental clutch began with the onset of pipping of the most advanced egg in the clutch.

<sup>b</sup> Sample size was reduced in experimentals at 30°C due to low hatchability.

For those eggs that hatched, pip-hatch intervals for controls were similar between the two years (Table 4). Mean pip-hatch intervals at 33°C increased above control levels by 10.0%, but this difference was not significant (unpaired  $t = 1.14$ ,  $df = 52$ ,  $P > 0.10$ ). At 30°C, mean pip-hatch intervals increased significantly, to 41.1% above the controls (Table 4) ( $t = 3.6$ ,  $df = 30$ ,  $P < 0.01$ ). Overall, there were no negative effects of chilling eggs in the laboratory down to 33°C, whereas both hatchability and pip-hatch intervals were adversely affected by chilling down to or below 30°C.

## DISCUSSION

Terminal-egg neglect was clearly present in Herring Gulls. Neglect resulted in a mean temperature drop of pipped c-eggs to about 33°C, more than 4°C below the temperature of pipped a-eggs. As reported previously for Black-headed Gulls (*L. ridibundus*) (Beer 1966), Herring Gulls (Drent 1970), and American White Pelicans (Evans 1989), neglect of terminal eggs occurred when parents began to brood and care for the first-hatched chicks within the brood. In contrast to earlier suggestions for gulls (Haycock and Threlfall 1975, Beer 1966, Reid 1987), we found no evidence that terminal-egg neglect was severe enough to lead to an increase in mortality of c-eggs during the final stages of incubation. Our experimental results from both field and laboratory suggest that there was no effect on embryonic or neonatal survival over a range of mean incubation temperatures between 33.0 and 37.8°C.

Our results also indicate that there were no neglect-induced hatching delays. In the field, pip-hatch intervals did not differ between neglected pipped c-eggs exposed to mean temperatures of about 33.5°C and unneglected c-eggs incubated at a temperature assumed to be similar to that of natural a-eggs, about 37.6°C. This field result was confirmed by a lack of difference in pip-hatch

intervals between late-stage embryos incubated in the laboratory at either 33.0 or 37.8°C. Paludan (1951) also rejected the notion that incubation disruptions retard hatching of c-eggs based on his finding that pip-hatch intervals at unmanipulated Herring Gull nests were not significantly different between a- and c-eggs. The absence of hatch retardation over the temperature range of 33–37.8°C suggests that late-stage Herring Gull embryos are well-adapted, physiologically, to withstand normal downward fluctuations in incubation temperature. A relatively low metabolic  $Q_{10}$  (1.55) over this same temperature range just prior to hatching (Drent 1970) also suggests a measure of temperature independence in this species. (See Bennett and Dawson, 1979, for a more striking example of temperature independence,  $Q_{10} = 1.1$  between 30–40°C, in Heermann's Gull, *L. heermanni* tested at 2–9 days of incubation).

The decrease in hatchability and increase in pip-hatch intervals when we chilled Herring Gull eggs to 30°C in the laboratory indicates that the critical lower developmental temperature for late-stage embryos of this species lies between 30 and 33°C. Development ceased when incubation temperature fell to 27°C, a temperature that has been described as "physiological zero" for domestic chicken embryos (Funk and Biellier 1944, see also Drent 1970).

Pip-hatch intervals in at least two other species, Ring-billed Gulls (*L. delawarensis*) (Evans 1990c) and American White Pelicans (Evans 1990b) are increased when pipped eggs are incubated in the laboratory at 33°C. Our present results suggest that Herring Gull embryos at the pipped egg stage are somewhat more cold hardy than these other species. Natural incubation temperature of Ring-billed Gull c-pip eggs is about 38°C (R. Evans, unpubl. data), and American White Pelicans maintain mean pipped terminal-egg temperature at  $37.8 \pm 0.3^\circ\text{C}$  (Evans 1990d), both above the temperature at which hatching

delays or mortality are induced in those species. Female passeriform birds also maintain mean egg temperatures above physiological zero (Haforn 1988), in this case by adjusting the duration of periodic foraging recesses from the nest. The possibility that calls of Herring Gull embryos in chilled pipped eggs are instrumental in fine-tuning parental incubation as in pelicans (Evans 1990d) remains to be tested.

Despite the absence of an effect of neglect on pip-hatch intervals, we did find a significant effect of neglect on within-clutch hatch asynchrony, a-c hatch intervals being shorter at control nests where c-eggs were subject to natural levels of neglect. Because shorter a-c hatch intervals may reduce the terminal chick's competitive disadvantage (Slagsvold 1985, Amundsen and Stokland 1988, Hebert and Barclay 1986), our results suggest that egg neglect may benefit the terminal offspring. In agreement with this interpretation, c-chicks that were exposed to natural levels of neglect as pipped eggs had significantly faster growth rates than chicks from un-neglected c-eggs. They did not survive better or achieve a significantly greater increase in weight by seven days, however, indicating that any benefit they may have received from neglect was marginal, at best.

The a-c hatch interval can be partitioned into two separate periods, that between the hatching of the a-egg and pipping of the c-egg, and the remainder lying between the pipping and hatching of the c-egg (pip-hatch interval). As discussed above, we found no significant effect of natural levels of neglect on pip-hatch intervals. Similarly, the a-hatch to c-pip intervals between experimental and control nests were not significantly different (Lee 1988). Evidently the significant difference in a-c hatch intervals resulted from the cumulative effects of these two time components, neither of which was significant in itself. The robustness of the positive effect of neglect on a-c hatch intervals and subsequent growth rate thus remains open to doubt. A repeat of the present field experiment with Ring-billed Gulls (Evans, unpubl. data) showed neither a reduction in c-egg pip-hatch intervals nor a reduction in a-c hatch intervals at nests where c-eggs were subject to neglect. Further experiments with Herring Gulls would be of value. Whatever the ultimate resolution of this issue, it is evident that neglected pipped c-eggs chilled down to about 33°C were not subject to any measurable *decrease* in sur-

ivorship or growth. The results of our field and laboratory studies thus unambiguously support the conclusion that terminal-egg neglect in Herring Gulls is benign and does not bring about a diminution of c-egg fitness.

C-chick survival through the critical first week of life was appreciably greater during our study (>80% survival of c-chicks to seven days in 1987 at unmanipulated nests) than in some previous years at Kent Island (e.g., 20% c-chick survival to five days, Hebert and Barclay 1986, see Burger 1984 for other examples of wide yearly variations in c-chick survival). It remains possible that the intensity of terminal-egg neglect in Herring Gulls varies in concert with the severity of food-related c-chick survival. Greater neglect could be caused, for example, by more time spent away from the nest foraging. Whether mortality reported for pipped c-eggs in Herring Gulls (Drent 1970; Haycock and Threlfall 1975; see also Beer 1962, 1966) represents abandonment associated with food scarcity or some other environmental variable, or is rather an indication that pipped-c-eggs that inadvertently die are more likely to be abandoned, requires further study.

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